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Phylogeny and classification of the parasitic bee tribe Epeolini (Hymenoptera: Apidae, Nomadinae)[1]

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ABSTRACT A generic-level cladistic analysis of the cleptoparasitic bee tribe Epeolini (Apinae: Nomadinae) is presented. One hundred and two characters of adult external morphology are identified and coded for 32 representatives of all genera and subgenera presently recognized within the tribe, along with five outgroup taxa. The resulting topology is used in the formation of a higher-level classification of the tribe. Four subtribes are characterized: Odyneropsina Handlirsch, Rhogepeolina new subtribe, Epeolina Robertson, and Thalestriina new subtribe. *Pseudepeolus* and *Triepeolus* are not supported as subgenera of *Doeringiella* and are elevated to generic rank. The subgenus *Trophocleptria* renders *Epeolus* sensu stricto paraphyletic and is synonymized. The group *Parammobates* is recognized as a subgenus of *Odyneropsis*. *Triepeolus epeolurus* new species (type locality, Michoacán, Mexico), is described and figured; it is remarkable for a number of autapomorphic traits, particularly those of the pseudopygidial area. A key to the genera of the tribe is provided. The taxonomic history of the tribe, as well as available information on hosts and biology of epeolines, is summarized. A review of pertinent morphological terminology is presented, with special emphasis on the sting apparatus.

Key Words: Bees, Apidae, Nomadinae, Epeolini

INTRODUCTION

The tribe Epeolini is a diverse assemblage of parasitic bees in the subfamily Nomadinae. The genera are primarily found in South America; however, the two most species-rich genera, *Triepeolus* and *Epeolus*, are widely distributed, with the latter found on all continents except Australia (and Antarctica). Epeolines parasitize a wide variety of distantly related bees in the families Colletidae (Colletinae and Diphaglossinae), Andrenidae (Oxaeinae), Halictidae (Nomiinae), and Apidae (Emphorini, Eucerini, and Anthophorini) (Rozen, 2001). The mode of parasitism in epeoline bees is typical for all known Nomadinae: the female enters an open cell while the host is away foraging, inserts her egg in a slit or hole in the cell wall, and departs. The egg hatches into a hospicidal first larval instar, equipped with long, sickle-shaped mandibles with which it kills the host egg or larva and consumes its intended provisions (Rozen, 1989b, 1991). According to the most recent classification (Michener, 2000), the tribe consists of six genera, several of which contain two or more subgenera or species groups (Table 1). As the result of the present analysis, I herein refer to *Doeringiella* sensu stricto, *D.* (*Pseudepeolus*), and *D.* (*Triepeolus*) (sensu Michener, 2000) as *Doeringiella*, *Pseudepeolus*, and *Triepeolus*, respectively.

This study was prompted by the discovery of a new species (described in Appendix 1) that combines some of the characters of the pseudopygidial area historically used to differentiate *Epeolus* from *Triepeolus*. Further investigations into the diversity of *Triepeolus* made apparent the need for a more robust understanding of epeoline phylogenetic relationships. The purpose of the present study is to resolve the phylogenetic relationships of the genera and subgenera within Epeolini.

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Table 1. Classification of the bee tribe Epeolini.

Michener (2000)	Present study
	SubtribeOdyneropsina
Genus ***Odyneropsis***	Genus ***Odyneropsis***
"Species group" *Odyneropsis*	Subgenus *Odyneropsis*
"Species group" *Parammobates*	Subgenus *Parammobates*
	Subtribe Rhogepeolina
Genus ***Rhogepeolus***	Genus ***Rhogepeolus***
	Subtribe Epeolina
Genus ***Epeolus***	Genus ***Epeolus***
Subgenus *Epeolus* s. stricto	
Subgenus *Trophocleptria*	
	Subtribe Thalestriina
Genus ***Doeringiella***	Genus ***Doeringiella***
Subgenus *Doeringiella* s. stricto	
Subgenus *Pseudepeolus*	Genus ***Pseudepeolus***
Subgenus *Triepeolus*	Genus ***Triepeolus***
Genus ***Rhinepeolus***	Genus ***Rhinepeolus***
Genus ***Thalestria***	Genus ***Thalestria***

London, and the loan of material from Berkeley. Scanning electron microscopy work at the American Museum of Natural History was generously arranged by Jerome G. Rozen, Jr., Angela Klaus, and Kevin Frishmann.

Specimens used in this study are primarily from the entomological collection of the University of Kansas Natural History Museum and Biodiversity Research Center (SEMC); other material was made available by the following institutions: Universidade Federal do Paraná, Curitiba (Favizia F. de Oliveira and Danuncia Urban)—*Rhogepeolus emarginatus*; Los Angeles County Museum of Natural History, Los Angeles (Roy Snelling)—*Triepeolus heterurus*; American Museum of Natural History, New York (Jerome G. Rozen, Jr., and Valerie Giles)—*Pseudepeolus fasciatus*, *Hexepeolus rhodogyne*, *Rhogepeolus plumbeus*, *Triepeolus lunatus*; United States National Museum of Natural History, Washington, D. C. (Maureen Melo)—*Triepeolus ancoratus*; The Natural History Museum, London (George Else and Christine Taylor); Kyushu University, Fukuoka (Osamu Tadauchi); and Maximilian Schwarz, personal collection, Ansfelden—*Triepeolus ventralis*; and Museum für Naturkunde, Berlin (Frank Koch)—*Parammobates brasiliensis*. Specimens of *Triepeolus epeolurus* were lent from the Estación de Biologia, UNAM, Chamela (EBCC, Ricardo Ayala), USDA-ARS Bee Biology and Systematics Laboratory, Logan, Utah (BLCU, Terry Griswold), Florida State Collection of Arthropods, Gainesville, Florida (FSCA, James Wiley), and the Essig Museum of Entomology, University of California, Berkeley, California (EMEC, Cheryl Barr). George Else is further acknowledged for arranging my visit to examine *Odyneropsis* types; Favizia F. de Oliveira is also thanked for information on specimens of *Odyneropsis* in Curitiba.

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HISTORICAL REVIEW

Latreille (1802) named the first epeoline genus, *Epeolus*, and placed it in the solitary division of the family Apiariae, along with *Nomada* and *Melecta*. More than 50 years later, Smith (1854) named *Thalestria* and placed it with a diverse group of bees (e.g., Megachilidae, Melectini, and Euglossini) in the subfamily Denudatae. *Doeringiella*, *Pseudepeolus*, and *Trophocleptria* were named by Holmberg (1886a, 1886c), who remarked on the morphological similarity of these genera to each other as well as to the brachynomadine genus *Brachynomada*, which he also described in the same year (Holmberg, 1886b). The distinctive genus *Odyneropsis* was described by Schrottky (1902); shortly thereafter Friese (1906) proposed the genus *Parammobates* for a related group.

Gribodo (1894) placed species of *Epeolus* with three maxillary palpal segments into the subgenus *Diepeolus* ("*Di-*" for the two articulations of the segments). He further proposed that, for the love of symmetry ("questo amore della simmetria"), those species with two palpal segments be named *Monoepeolus*. This idea was echoed by Robertson (1901), who proposed the genus *Triepeolus* for those *Epeolus* with three maxillary palpal segments. Although it is now known that palpal segment number does not reliably differentiate *Triepeolus* from *Epeolus*, Robertson was fortunate to include species that are morphologically distinct from *Epeolus* in his generic description of *Triepeolus*. Several of these other characters, including the female pseudopygidial area and sixth sternum, were soon recognized by Robertson (1903), yet he still used maxillary palpal segment number to differentiate genera. This is exemplified by his 1903 proposal of the genus *Argyroselenis*, which was based on a species with female pseudopygidial area and sixth sternum characteristics of *Epeolus*, but which also had three maxillary palpal segments. Thus, Robertson's *Argyroselenis* is synonymous with Gribodo's *Diepeolus*, which in turn is synonymous with *Epeolus*. Similarly misleading characters caused other workers (e.g., Ashmead, 1899; Cockerell, 1921; and Mavromoustakis, 1954) to recognize other epeoline groups that have since been synonymized.

Using the diagnostic characters given by Robertson (1903), Bischoff (1930) was the first to place Old World epeolines (*Triepeolus tristis* and *Epeolus tsushimensis*) into the genus *Triepeolus*; however, the latter species has been shown to belong to the genus *Epeolus* (Rightmyer, in press).

Grütte (1935) proposed the close relationship of the epeoline genera (although he considered *Doeringiella*[2] to be synonymous with *Brachynomada*), and excluded from them a great number of taxa that had been previously grouped with them (e.g., *Ammobates*, *Ammobatoides*, *Biastes*, *Coelioxoides*, *Holcopasites*, *Isepeolus*, *Leiopodus*, and *Osiris*, as well as the parasitic melectine and megachiline genera). Based primarily on characters of the mouthparts, wings, and female S6, Grütte considered *Odyneropsis* to be a basal member of the group, and hypothesized that *Thalestria* and *Triepeolus* were more closely related to each other than to the other epeoline genera; in fact, he suggested that *Thalestria* might be a "modified" *Triepeolus*. He further proposed the synonymy of *Parammobates* with *Odyneropsis*, observing that the only significant difference between the two appeared to be size.

Linsley and Michener (1939) provided a comparative study of adult nomadine morphological structures, particularly of male and female terminalia, and recognized Nomadini and Epeolini as separate tribes within the family Nomadidae. Michener (1944) placed the phylogenetic position of Epeolini in a more robust analysis of bees as a whole, and in 1954, proposed the close relationship of most of the genera now considered to be in the subfamily Nomadinae. Concurrently, Moure (1954, 1955) produced the first concentrated studies of South American epeolines since Holmberg. Moure (1954) proposed the subgenera *Doeringiella* (*Stenothisa*) and *D.* (*Orfilana*), the latter of which was proposed for species whose males lack swollen scapes and whose females have conspicuous pseudopygidial areas. Moure (1955) gave an account of the species of *Odyneropsis* and described three new epeoline genera from South America; these genera, *Rhinepeolus*, *Rhogepeolus*, and *Coptepeolus*, are the last epeoline genera to have been named.

Since Moure (1955), the majority of the systematic work on adult Epeolini has been done by Roig-Alsina, who has undertaken a series of revisions of the species of the South American genera. Roig-Alsina (1989) revised and determined the phylogenetic relationship of the species of *Doeringiella*. Based on this analysis, he concluded that swollen male scapes independently originated twice within *Doeringiella*; however, a more extensive analysis by Compagnucci and Roig-Alsina (2003) placed such males together as a single clade. Roig-Alsina (1996) expanded the generic definition of *Rhogepeolus* to include the monotypic *Coptepeolus* along with two other closely allied species. In 2003, he revised *Pseudepeolus* and provided a phylogenetic hypothesis of the genus and its close relatives. Michener (2000) proposed the subgeneric status of *Triepeolus* and *Pseudepeolus* under *Doeringiella* based on observations communicated to him by Roig-Alsina; these observations were more fully enumerated by Roig-Alsina (2003). Michener (2000) also recognized *Trophocleptria* as a subgenus of *Epeolus*.

Treatment of *Epeolus* has been limited to various geographical regions; they are Mitchell (1962) for eastern North America, Brumley (1965) for western North America, Eardley (1991) for sub-Saharan Africa, Bischoff (1930) and van Lith (1956) for the Palearctic, Richards (1937) for Great Britain, and Yasumatsu (1933) and Hirashima (1955) for Japan.

The phylogenetic position of Epeolini within Nomadinae has been addressed by a number of studies based on adult and mature larval data sets (Alexander, 1990, 1996; Roig-Alsina, 1991; Roig-Alsina and Michener, 1993; Rozen, 1996; Rozen et al., 1978, 1997). While these studies have not unambiguously resolved the sister taxon to Epeolini, they have shed some light on which tribes are likely to be closely related. These tribes are characterized by a particular type of female S6, termed the "nomadine type" by Roig-Alsina (1991), in which the lateral lobes bear spine-like setae as opposed to forming two conical points. The taxa characterized by this type of S6 are the tribes Ammobatoidini, Biastini, Brachynomadini, Epeolini, Hexepeolini, Nomadini, and Townsendiellini. All of these tribes, except for Biastini and Townsendiellini, have been supported as sister to Epeolini in the studies cited above, depending upon what taxa and characters are used to create the phylogenetic hypothesis (see Table 3). Other topologies obtained by these authors resolved Epeolini nested within the phylogeny, such that a sister taxon was resolved for Epeolini plus a clade containing several other tribes. In these cases, either *Hexepeolus* (Rozen, 1996) or *Nomada* (Rozen, 1996; Rozen et al., 1997) was resolved as the sister taxon to the clade composed of Epeolini and other nomadine tribes. As discussed by Rozen (1996), the wide variety of phylogenetic hypotheses proposed by these authors is likely reflective of the fact that different taxa and character sets were employed in each study.

The biology of most epeoline species remains largely unknown; however, studies of egg, larval, and pupal morphology and modes of parasitism (some of them comparative) were provided by Claude-Joseph (1926) for *Doeringiella*; Michener (1953), Rozen (1966, 1989b), Rozen and Favreau (1968), McGinley (1981), and Torchio and Burdick (1988) for *Epeolus*; Rozen (1996) for *Thalestria*;

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[2] Grutte seemingly did not observe any specimens of *Doeringiella*, and perhaps relied on published descriptions instead. It is interesting that he considered *Brachynomada* to be so closely allied to epeolines. He apparently considered the genus to be somewhat of an anomaly, and hesitated to place *Brachynomada* in a specific relationship to the epeoline genera. However, he may well have misidentified *Brachynomada*, a genus that does not closely resemble Epeolini, as well as perhaps *Doeringiella*.

Table 2. Number of species, geographical distribution, and host records for genera of Epeolini

Genus	No. of species	Geographic distribution	Hosts
Odyneropsis	12	Neotropical; 1 sp. in southwest USA	*Ptiloglossa* (Colletidae)
Rhogepeolus	5	South America	Unknown
Epeolus	ca. 110	Worldwide, excluding Australia, tropical India, southeast Asia	*Colletes* (Colletidae)[2]
Doeringiella	35	South America	Eucerini (Apidae), possibly *Diadasia* (Apidae), *Caupolicana* (Colletidae)
Pseudepeolus	5	South America	Unknown
Rhinepeolus	1	South America	Unknown
Triepeolus	ca. 150	New World; 1 sp. each in Europe and Asia	Eucerini (Apidae), *Anthophora, Centris, Melitoma*[3] (Apidae), *Ptiloglossa* (Colletidae), *Protoxaea* (Andrenidae), *Dieunomia* (Halictidae)
Thalestria	1	Neotropical	*Oxaea* (Andrenidae)

[1] Information in this table is modified from Michener (2000) and Roig-Alsina (2003).
[2] Medler (1980) included *Tetralonia* (Eucerini) in his host list of *Epeolus*; this host association seems dubious.
[3] The *Melitoma* host record is for *Triepeolus donatus* entering the nest of *Melitoma taurea*, observed by W. H. Ashmead, who incorrectly concluded that the former species was the builder the nest (Robertson, 1899); this host record is not well supported. The likely host of *T. donatus* in New York is *Melissodes desponsa* (J. S. Ascher, in lit.)

Mayet (1875)[3], Graenicher (1905), Michener (1953), Bohart (1966, 1970), Rozen (1966, 1984, 1989b), Nielsen and Bohart (1967), McGinley (1981), Torchio (1986), and Wuellner and Hixon (1999) for *Triepeolus*; and Rozen (1966) for *Odyneropsis*. Rozen (1989b) highlighted characters of first larval instars that serve to differentiate several species of *Epeolus* and *Triepeolus*. Information on various epeoline taxa can also be found in Rozen's (2001) key to the mature larvae of parasitic genera and his (2003) listing of the number and size of mature oocytes and the ovariole number of parasitic taxa.

Host associations for some epeoline genera have been known more than a century (e.g., Robertson, 1901). In contrast, the hosts of other genera (e.g., *Rhogepeolus, Rhinepeolus*) remain unknown or speculative. A summary of currently known host records for epeoline genera is found in Table 2.

METHODS AND MATERIALS

Morphological terminology follows that proposed by Michener (1944, 2000), except for certain terminology proposed by Michener and Fraser (1978) for mandibular structure, Engel (2001) for wing veins, Roig-Alsina (1991) for female S6, and Scudder (1961) and Packer (2003) for female genitalia and associated internal terga, respectively. Specimens were examined, measured, and illustrated using an Olympus SZX9 dissection microscope, ocular micrometer, and drawing tube. Photomicrographs were taken using a MicrOptics ML-1000 Digital Imaging System. Scanning electron micrographs were produced using a Hitachi S4700 Field Emission SEM with uncoated specimens. Dissected male and female terminalia were cleared using potassium hydroxide at room temperature and stored in glycerin.

The following morphological abbreviations are used in the text: flagellar segment (F), metasomal tergum (T), metasomal sternum (S), and ocellar diameter (OD).

Thirty-seven taxa, including five outgroup taxa, were used in this study (Table 3). The tribes used as outgroup taxa are those identified by Roig-Alsina (1991) as belonging to the lineage characterized by the "nomadine-type S6," excluding Townsendiellini. When possible, an attempt was made to choose a basal genus within each of the outgroup tribes, and additional preference was given to New World species, given the preponderance of epeoline genera from the Western Hemisphere. Specifically, *Brachynomada* sensu stricto is a South American subgenus, *Holcopasites* is the only New World genus of Ammobatoidini, and *Hexepeolus rhodogyne*, the only species of Hexepeolini, is known from California and Arizona, USA. *Nomada pampicola* belongs to the *vegana* group of Alexander (1994), as well as to the genus *Hypochrotaenia* recognized by Snelling (1986). Michener (2000) hypothesized that the *vegana* group is basal within *Nomada*, due to the fact that this Neotropical group parasitizes a more closely related group (i.e., *Exomalopsini*) than do other groups of *Nomada* (although this hypothesis is somewhat controversial and was not supported by the phylogenetic study undertaken by Alexander, 1994). Unfortunately, material of the Nearctic genera *Rhopalolemma* and *Neopasites* was scarce; instead, the Palearctic genus *Biastes* was used as an exemplar for Biastini.

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[3] It is possible that Mayet was describing a species of *Epeolus* in this paper; she considered *Triepeolus tristis* to be synonymous with *Epeolus luctuosus* and *Epeolus speciosus* (p. 81), and the bee she observed was parasitizing nests of *Colletes*.

An attempt was made to include a morphologically and geographically diverse group of exemplar species for each of the recognized genera and subgenera of Epeolini. Exemplar species of *Doeringiella* were chosen to represent different clades in the phylogeny for the group presented by Roig-Alsina (1989). A minimum of two females and two males were examined for each taxon, with the exception of *Rhogepeolus emarginatus*, for which only one male and female were available.

Many of the characters used in the present phylogenetic analyses were taken or modified from characters discussed by Moure (1955), Roig-Alsina (1989, 1991, 2003), Alexander (1990), and Michener (2000). An annotated list of the 102 characters used in the phylogenetic reconstructions can be found in Appendix 2. The matrix of character codings is located in Appendix 3. Forty-four of the characters are multistate. Characters not applicable to certain taxa are coded as "-"; there are no missing data. All characters are unweighted and all but 10 are nonadditive. The additive characters are 2, 11, 13, 18, 23, 24, 50, 59, 75, and 98, and were selected based on the ability to identify a logical evolutionary sequence for the character states (e.g., a maxillary palpus might logically evolve from containing six palpal segments to five palpal segments before evolving to contain fewer segments.) The plesiomorphic state was not identified a priori and thus character states numbered zero are not implied to be plesiomorphic. The matrix was constructed in WinClada, version 1.00.08 (Nixon 2002). The phylogeny was created in NONA (Goloboff 1993) using an unconstrained heuristic search [Multiple TBR+TBR (mult*max*) search strategy]. The search parameters were 10,000,000 maximum trees to keep, 1000 replications, 1 starting tree per replication, and 0 random time.

Four phylogenetic analyses are presented. The first used all of the taxa listed in Table 3 and characters listed in Appendix 2. The second, third, and fourth analyses were restricted to only those taxa listed under Thalestriina in Table 1, with the addition of different outgroup taxa. In the second analysis, *Epeolus natalensis* was used as the outgroup based on its basal position in *Epeolus* (which in turn was the sister taxon of Thalestriina) in the first phylogenetic analysis. All *Epeolus* species listed in Table 3 except for *Epeolus bifasciatus* and *Epeolus variolosus* (i.e., *Trophocleptria* species sensu Michener, 2000) were used as the outgroup in the third analysis. The fourth analysis included all *Epeolus* species listed in Table 3. With the taxa thus restricted, uninformative characters were deactivated in WinClada. In the end, the second phylogenetic analysis employed 20 taxa and 41 characters, seven of which were additive. The third had 26 taxa and 66 characters, 10 of which were additive; the fourth had 28 taxa and 69 characters, 10 of which were additive. The analysis of these restricted data sets then proceeded as described for the first.

Table 3. Taxa included in the phylogenetic analyses, with locality data associated with examined specimens in parenthesis following names. Footnotes 1–4 give references to studies that support the sister-group relationship of these taxa to the tribe Epeolini.

Outgroup taxa

Ammobatoidini:[1] *Holcopasites calliopsidis* (Linsley) (midwestern USA)
Biastini: *Biastes brevicornis* (Panzer) (Slovak Republic)
Brachynomadini:[2] *B.* (*Brachynomada*) *scotti* Rozen (Peru)
Hexepeolini:[3] *Hexepeolus rhodogyne* Linsley and Michener (southwestern USA)
Nomadini:[4] *Nomada pampicola* Holmberg (Argentina)

Ingroup taxa: Epeolini

Doeringiella: *Doeringiella. bizonata* Holmberg (Argentina), *D. cingillata* Moure (Brazil), *D. crassicornis* (Friese) (Argentina), *D. crinita* Roig-Alsina (Argentina), *D. holmbergi* (Schrottky) (Argentina)
Epeolus: *Epeolus bifasciatus* Cresson[5] (Kansas, USA), *E. compactus* Cresson (Mexico). *E. cruciger* (Panzer) (Slovak Republic), *E. lectoides* Robertson (New York, USA), *E. mesillae* (Cockerell) (southwestern USA), *E. natalensis* Smith (South Africa), *E. schummeli* Schilling (Slovac Republic), *E. tarsalis rozenburgensis* van Lith (Netherlands), *E. variolosus* Holmberg[5] (Argentina)
Odyneropsis:[6] *O.* (*Odyneropsis*) *armata* (Friese) (Argentina, Brazil), *O.* (*Parammobates*) *batesi* Cockerell[7] (Panama)
Pseudepeolus:[8] *Pseudepeolus fasciatus* Holmberg (Argentina, Brazil)
Rhinepeolus: *Rhinepeolus rufiventris* Moure (Argentina)
Rhogepeolus:[9] *Rhogepeolus bigibbosus* Moure (Argentina), *R. emarginatus* (Moure) (Brazil)
Thalestria: *Thalestria spinosa* (Fabricius) (Bolivia, Brazil)
Triepeolus: *Triepeolus ancoratus* Cockerell (California, USA). *T. distinctus* (Cresson) (Arizona, USA), *T. epeolurus* Rightmyer (central, southern Mexico), *T. heterurus* (Cockerell and Sandhouse) (California, USA), *T. kathrynae* Rozen (Mexico), *T. lunatus* (Say) (Kansas, New Jersey; USA), *T. nobilis* (Friese) (Brazil), *T. quadrifasciatus* (Say) (Texas, USA), *T. tristis* (Smith) (Austria, Italy, Slovak Republic), *T. ventralis* (Meade-Waldo) (China, Japan), *T. vicinus* (Cresson) (Cuba)

[1] Rozen, 1996 [adult and larval characters].
[2] Roig-Alsina, 1991 [adult characters, primarily female S6]; Roig-Alsina and Michener, 1993 [adult and larval characters]; Alexander, 1996 [adult characters].
[3] Alexander, 1990 [adult characters, excluding female S6].
[4] Rozen et al., 1997 [larval characters].
[5] These species of *Epeolus* belong to the subgenus *Trophocleptria* of Michener's (2000) classification.
[6] The lectotype of *Parammobates brasiliensis* Friese, type species of *Parammobates*, was also examined.
[7] Based on the species description, it is likely that this species is synonymous with *Odyneropsis columbiana* Schrottky; however, only the holotypes for *Odyneropsis* (*Parammobates*) *batesi* (type locality: Ega, Brazil) and its subspecies *Odyneropsis* (*Parammobates*) *batesi veseyi* Cockerell have been examined. I have also examined material of *O.* (*P.*) *batesi* from Ecuador in the collection of Donald Baker. *Odyneropsis columbiana* is known from Colombia, while *O.* (*P.*) *batesi veseyi* is known from Trinidad.
[8] A male specimen of *Pseudepeolus angustata* (Moure) was also examined.
[9] Specimens of *Rhogepeolus plumbeus* (Ducke) (Brazil) and *Rhogepeolus rozenorum* Rightmyer (Peru) were also examined.

Under Systematics (below), the genera and subtribes recognized herein are diagnosed primarily on the basis of characters used in the phylogenetic analyses. These characters are followed by a number (the character) and a number in parentheses (the character-state), which correspond to numbers in the character matrix found in Appendix 2. Other diagnostic characters are mentioned that were not included in the phylogenetic analyses; these do not have associated character and character-state numbers.

MORPHOLOGY

In this section I discuss morphological structures that are specific to nomadine bees and thus might be poorly known by many systematists not working directly with this group. In addition, I discuss the morphological terminology used herein that is either new or little used in the bee literature.

PSEUDOPYGIDIAL AREA

In female Nomadinae, the dense field of setae borne medioapically on T5 is termed the pseudopygidial area, so named because this region of modified setae often resembles the overall shape and position of a pygidial plate. This area is likely homologous to the prepygidial fimbria found in other bees (Michener, 2000), which in those bees possibly functions as a means of gathering loose sand from the nest (Grütte, 1935). The setae of the pseudopygidial area generally are simple (i.e., not branched) and are variously modified into a wide array of morphologies. A survey of the remarkable diversity of the setae found in the pseudopygidial region is presented in Figs. 179–191 (see also Rozen, 1989a). The setae lateral and basal to the pseudopygidial area are usually branched. The function of the pseudopygidial area is not known, although the setae of this area are frequently reflective, perhaps because they are unbranched and flattened. In many epeolines, the pseudopygidial setae resemble those found on the posterolateral corner of the metatibia.

STING APPARATUS

The sting apparatus is a complex assemblage of tergal, sternal, and genital sclerites. A generalized representation of the sclerites of the sting apparatus, their synonymous names, and their articulations are shown in Figure 1 for the genus *Triepeolus*. In nomadine bees, these sclerites are articulated such that the sting and processes of the S6 are able to achieve a certain amount of mobility and flexibility. These structures attain even greater mobility in some epeoline genera primarily due to two morphological adaptations. Within Thalestriina (especially *Thalestria* and some *Triepeolus*), the disk of the female S6 is greatly reduced, and is positioned basally on the sternum relative to the mediolateral apodemes (Figs. 7, 9, 10, and 22B). Consequently, the processes are much less restricted in their ability to move in more than one plane. Also, within Thalestriina (*Doeringiella*, some *Triepeolus*, and especially in *Thalestria*) the lateral process of T7 (i.e., the part that articulates with S6) is elongate (Figs. 1, 162, and 163). This elongation allows the S6 as a whole to be extruded further from the apex of the metasoma than would otherwise be possible.

The ventralmost sclerite associated with the sting apparatus is the S6 (Fig. 1). The S6 is a highly modified and character-rich structure in nomadine bees, and presumably plays a role in their particular mode of parasitism. The structure possibly serves a tactile function for the female to orient herself in the cell, and likely helps to position the parasitic egg within the cell wall of the host nest, as a means of transferring the egg from the ovipore to the cell wall. Roig-Alsina (1991) identified, named, and established the homologies of several structures of the S6; other features are named herein. The various structures of the S6 are labeled in Figures 2 and 7. The apical margin is generally characterized by a median emargination coupled with an elongation of the lateral margins, resulting in the formation of lateral apical processes. The extents to which the median emargination and lateral processes are formed vary dramatically within the subfamily and they are essentially absent in at least some *Nomada*. In some nomadines, principal setae are born on the ventral apical margin of the lateral processes, and are usually easily distinguished from other setae by their stout appearance. Such ventral setae are absent in *Brachynomada*. A patch of dorsoapical setae is also usually present and these setae are likewise somewhat stouter than most other setae found on the S6. In some nomadines, including Epeolini, the principal and dorsoapical setae are separated by flattened integument, termed the apical plate. Additionally, nomadines can have a row of setae flanking both the inner and outer margins of the lateral apical processes. These are termed the marginal setae and lateral series of setae, respectively. The lateral margin of the S6 bears a dorsally directed process that serves as an articulation point with the T7, termed the mediolateral apodeme. Once the S6 has been dissected and disarticulated from the T7 and sting, the S6 of many bees flattens into a more two-dimensional structure. This flattening is caused by the inward rotation of the lateral apical processes and the resultant outward, lateral rotation of the mediolateral apodemes (as shown in Figs. 5, 7, and 11); these apodemes are directed dorsally in life. As in other metasomal sterna, basal apodemes are found on the S6. In many Epeolini, the basal apodeme bears a finger-like projection on its median margin, termed the digitiform appendage of the basal apodeme (Fig. 7, DBA). A similar but nonhomologous structure is found on the basal margin of the disk of the S6 in some other Nomadinae. When this basal margin is laterally sclerotized, the sclerotization is termed the basolateral sclerotic band of the disk (Fig. 2, BSB).

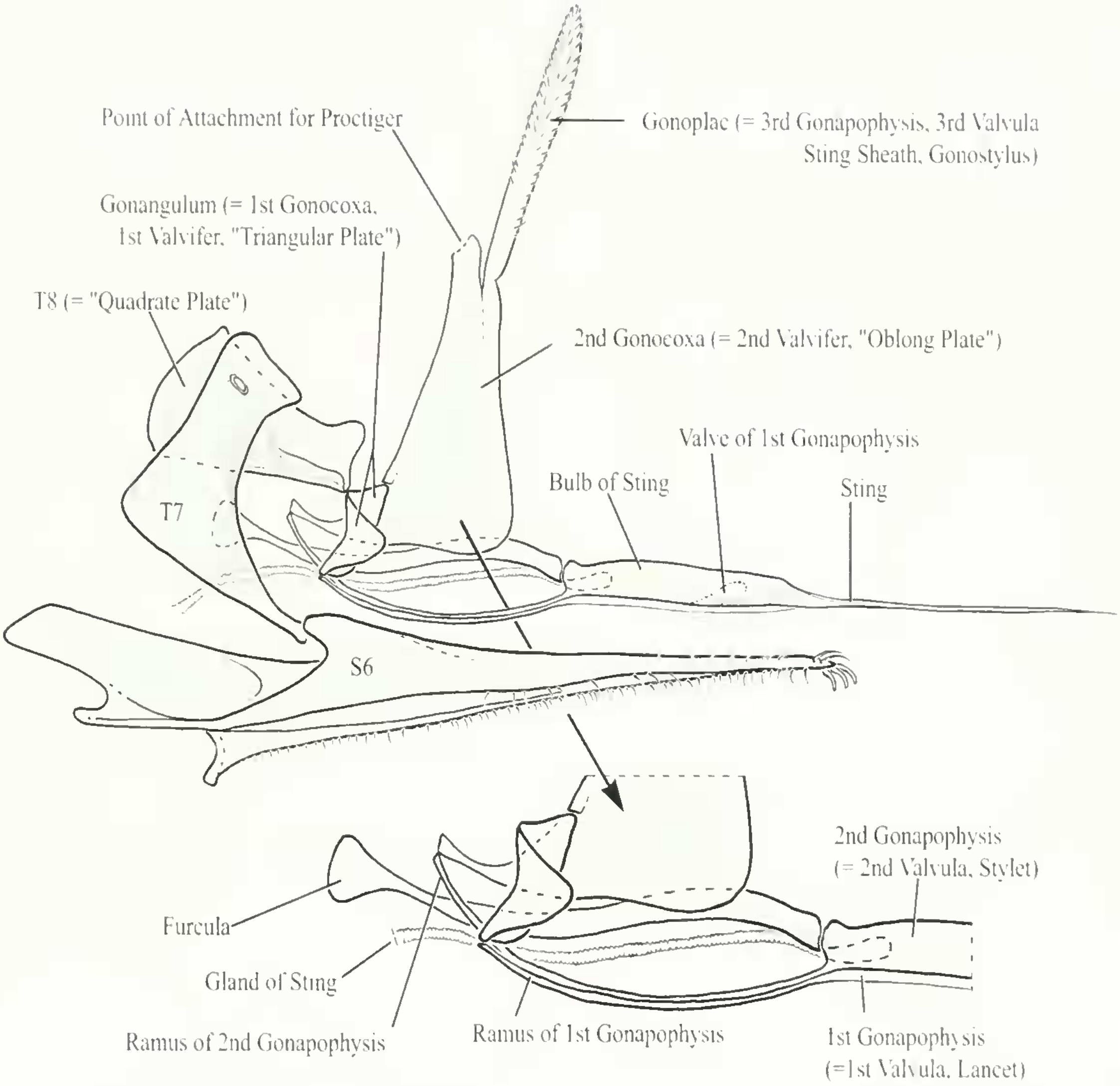
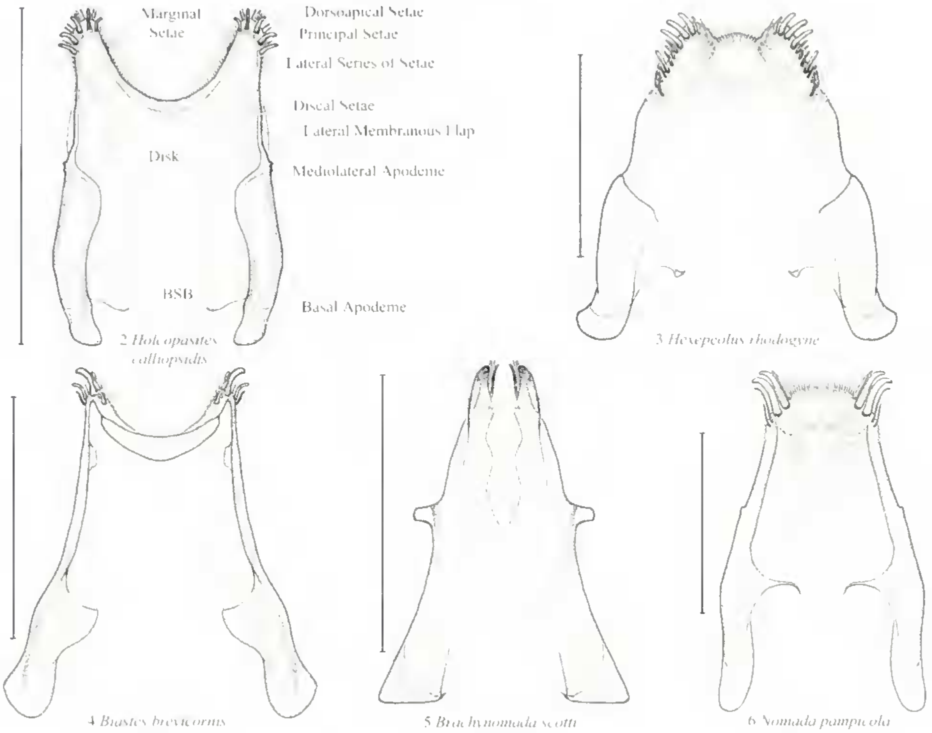

Point of Attachment for Proctiger
Gonoplac (= 3rd Gonapophysis, 3rd Valvula Sting Sheath, Gonostylus)
Gonangulum (= 1st Gonocoxa, 1st Valvifer, "Triangular Plate")
T8 (= "Quadrate Plate")
2nd Gonocoxa (= 2nd Valvifer, "Oblong Plate")
Valve of 1st Gonapophysis
Bulb of Sting
Sting
T7
S6
2nd Gonapophysis (= 2nd Valvula, Stylet)
Furcula
Gland of Sting
Ramus of 2nd Gonapophysis
Ramus of 1st Gonapophysis
1st Gonapophysis (=1st Valvula, Lancet)

Fig. 1. Sclerites of the sting apparatus of a generalized *Triepeolus*, with synonymous terminology given in parentheses. See Morphology section of text for further explanation.

A close inspection of the epeoline female S6 reveals that it appears to be composed of two distinct sclerites; one that includes the basal apodeme and extends up the outer surface of the lateral apical process, and one that includes the central disk of the S6 and extends up the inner surface of the lateral apical process. These sclerites are probably the result of subsegmentation of the S6 to allow for the particular conformation of that sternum.

Within Epeolini, certain female S6 morphologies are highly suggestive of functions related to particular modes of parasitism. In Thalestriina, the claw-like principal setae are suggestive of a digging or tactile function, as discussed above. The modifications for increased S6 mobility also suggest such a function. In *Epeolus*, the principle setae are modified into pointed denticles and the processes that bear these denticles are more rigidly attached to the disk of the sternum (Fig. 13). Both of these features suggest a saw-like function, and might have evolved in response to the cellophane-like lining that coats the cell wall of its host, *Colletes*. Observations reported by Torchio and Burdick (1988) support the idea that the *Epeolus* S6 is used in such a manner.

In addition to the largely internalized S6, two completely internalized tergal sclerites are each present as lateral hemitergites, as in other bees. The outermost hemitergite, T7, bears a spiracle and articulates with S6 ventrally (Figs. 1, 14, and 152–165). The region that articulates with the mediolateral apodemes of the S6 was termed the lateral process by Packer (2003). In the same work, Packer identified the region that would be oriented basolaterally in an undivided tergum; this region was termed the apodemal region. Similarly, the lateral margin was identified as the



2 *Holcopasites calliopsidis*

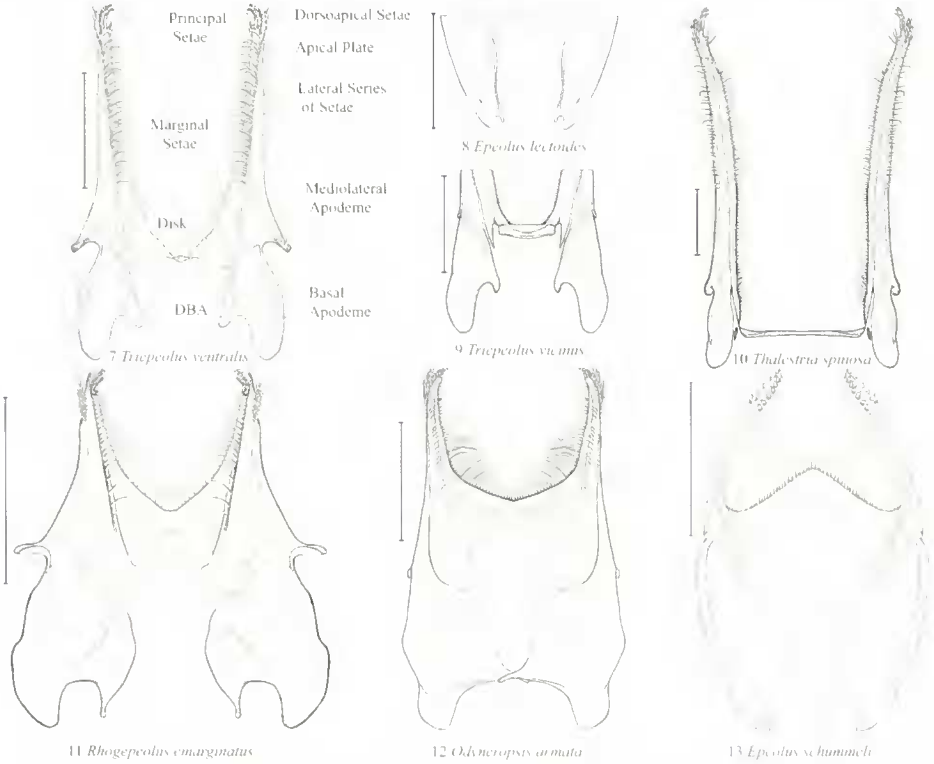
3 *Hexepeolus rhodogyne*

4 *Biastes brevicornis*

5 *Brachynomada scotti*

6 *Nomada pampicola*

Figs. 2–6. Sixth sterna of female Nomadinae, ventral view. Scale bars = 1 mm. BSB = Basolateral sclerotic band.



7 *Triepeolus ventralis*

8 *Epeolus lectoides*

9 *Triepeolus vicinus*

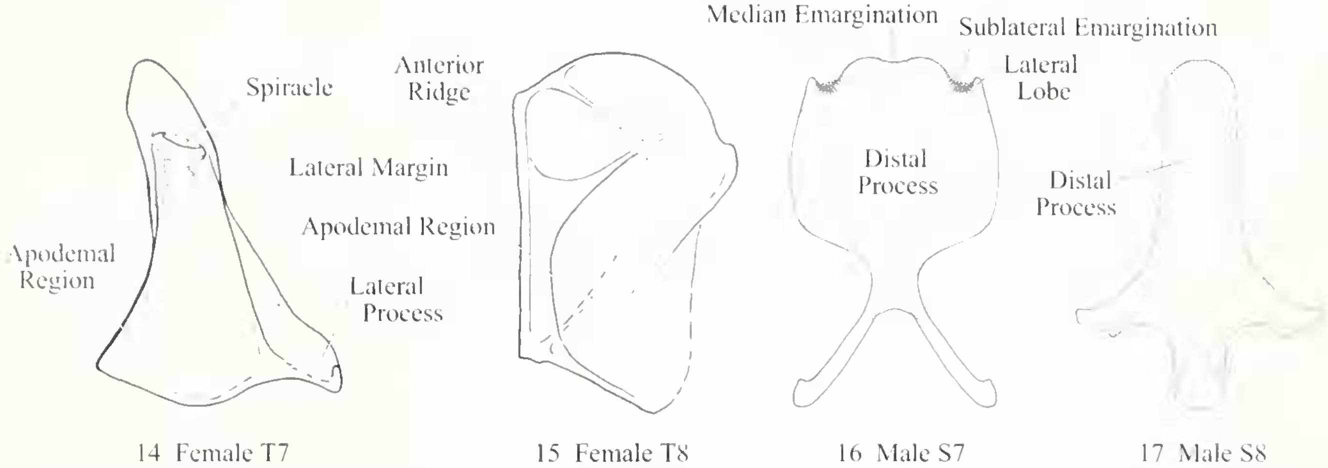
10 *Thalestria spinosa*

11 *Rhogepeolus emarginatus*

12 *Odyneropsis armata*

13 *Epeolus schummeli*

Figs. 7–13. Sixth sterna of female Epeolini, ventral view (Figs. 8 and 9, basal portion of sterna only). Scale bars = 1 mm. DBA = Digitiform appendage of the basal apodeme.



14 Female T7 15 Female T8 16 Male S7 17 Male S8

Figs. 14–17. Labeled internal sclerites of the metasoma. 14 and 15. Lateral view. (Lateral process of female T7 articulates with S6; lower left angle of female T8 articulates with gonangulum.) 16 and 17. Ventral view.

margin that extends toward the spiracle from the lateral process. These regions are labeled in Fig. 14. The innermost hemitergite, T8, lacks a spiracle and articulates with the gonangulum ventrally (Figs. 1, 15, and 147–151). The anterior ridge, as termed by Packer (2003), marks the margin bordered by the apodeme of the T8 (Fig. 15). Dorsally, T7 and T8 are connected by conjunctival membrane.

In nomadine bees, the gonangulum is a small, triangular sclerite that is produced medially into an enlarged flap bordered by a carina. The gonangulum articulates with the T8, second gonocoxa, and ramus of the first gonapophysis (Fig.1). The gonangulum has been termed the first valvifer or gonocoxa by many authors due to its articulation with the ramus of the first gonapophysis. However, Scudder (1961, 1964) has shown that the gonangulum is derived from a portion of the second gonocoxa. Evidence to support this hypothesis comes primarily from his ability to follow the evolution of the gonangulum throughout Dicondylia based upon its three consistent articulations with ninth abdominal tergum (metasomal T8), the second gonocoxa, and the first gonapophysis—from Zygentoma, where the affinity of the gonangulum with the second gonocoxa is apparent (also observed in *Thermobia* by Michener, 1944), to the more derived orders where the gonangulum becomes fused with a variety of structures (e.g., the ninth abdominal tergum and first gonocoxa). Additional developmental evidence supports the hypothesis that the gonangulum is derived from the second gonocoxa (Scudder, 1964). The first gonocoxa is apparently missing in all Hymenoptera, except perhaps in the Chalcidoidea (Scudder, 1961).

The second gonocoxa is a large sclerite that basally articulates with the gonangulum and ramus of the second gonapophysis (Fig. 1). Apically, it gives rise to the gonoplac; dorsally and apically it is associated with the weakly sclerotic distal sections of the hindgut.

In bees, the gonoplac is a setose structure that encases the sting when it is not in use. Its synonymous names are sting sheath, third gonapophysis or valvula, and gonostylus. Scudder (1961) proposed the term gonoplac to refer to a structure that is positionally homologous to a gonostylus, but which is formed of an outgrowth of the second gonocoxa (as opposed to the gonostylus, which is a moveably attached process of the gonocoxa). The reasons for and against the use of gonoplac as opposed to the other proposed terms were outlined by Scudder (1961, 1971) and will be briefly recounted here. The term sting sheath is not preferred because it obscures the homology of the structure with that of organisms in which it forms a part of the ovipositor (e.g., Gryllidae), rather than a sheath for the ovipositor or sting. The terms third gonapophysis or valvula are not preferred because they imply knowledge of a serial homology of the gonoplac with the first and second gonapophyses, which in turn are likely homologous with eversible vesicles found on the pregenital segments of Archaeognatha. This seems unlikely because both the gonoplac and second gonapophysis arise from the second gonocoxa. However, if the gonapophyses are homologues of eversible vesicles, as has been suggested by Scudder (1961), then the evidence for the homology of the gonoplac with the gonapophysis is somewhat inconclusive: while *Neomachilis* has only one pair of eversible vesicles per abdominal segments 2–7, *Petrobius* pregenital segments bear two pairs of eversible vesicles per segment. Given the apparently derived position of *Neomachilis* and *Petrobius* within the Machilidae (Sturm and Machida, 2001), it would perhaps be more informative to examine more basal members of the Machilidae and Meinertellidae to determine the groundplan number of eversible vesicles. Alternatively, it might be possible that the gonoplac represents an eversible vesicle of the tenth abdominal segment which subsequently moved onto the ninth.

The term gonostylus implies the homology of the structure with the styli found on the pregenital segments of Archaeognatha and Zygentoma, which in turn are presumably homologous with the telopodites or possibly the coxal styli of the thoracic legs. Scudder (1971) concluded that both gonostyli and gonoplacs are present in some insect orders, but that only gonoplacs are present in Hymenoptera. Although Scudder believed that female Hymenoptera lack gonostyli, it seems feasible that the structure found in this order is homologous to the styli of archaeognathan pregenital segments; after all, female hymenopteran genitalia resemble that of Archaeognatha in other ways (Scudder, 1961). Segmentation or pseudo-segmentation of the gonoplac has been observed in a number of bee groups, and apparent full articulation of the gonoplac with the second gonocoxa has been observed in wasps closely related to bees (Packer, 2003). Alternatively, it may be that the gonoplac in bees represents a composite structure of both an outgrowth of the second gonocoxa and an apical gonostylus. An additional component of the debate over terminology is that the term gonostylus implies the homology of the male and female genital parts bearing this name, which is supported by studies of gynandromorphic bees (Michener, 1944). Further study of this structure is needed to identify its homologs in the other insect orders and between the sexes, should they exist.

The sting is composed of three interlocking entities: a dorsal second gonapophysis (formed of two fused gonapophyses), and two ventral, unfused first gonapophyses (Fig. 1). Each first gonapophysis is equipped with a dorsal valve which, in bees, serves to force venom from the venom gland outward through a channel formed by the interlocking gonapophyses (Snodgrass, 1956). The first and second gonapophyses are anteriorly produced into slender rami, which articulate with the gonangulum and second gonocoxa, respectively. Finally, the second gonapophysis dorsally articulates with the furcula, which is a long, posteriorly bifid sclerite.

MALE INTERNAL SCLERITES

As in other bees, the seventh and eighth sterna of males are highly reduced and internalized in nomadines. A distal process is formed on both the S7 and S8 of some Nomadinae, including Epeolini (Figs. 16, 17, and 54–127). On the S7, the apical margin of the distal process is sometimes medially or sublaterally emarginate. In some epeolines, the apical margin is laterally extended into lobes. The presence of these emarginations and lobes, and their relative sizes, are diagnostic characters for separating males of the various epeoline genera, including *Epeolus* from *Triepeolus* (see Key to Genera, below).

PHYLOGENETIC RESULTS

In the phylogenetic analysis of all Epeolini, a heuristic search found 396 equally parsimonious trees (L = 383, CI = 43, RI = 74). The strict consensus of those trees (Figs. 18–19; L = 404, CI = 41, RI = 71) caused the collapse of 11 nodes. The phylogenetic relationships resolved by this analysis are discussed under Systematics (below).

The three restricted analyses of Thalestriina were highly affected by outgroup choice and produced incongruous topologies. The analysis that employed *Epeolus natalensis* as the outgroup produced 90 equally parsimonious trees (L = 125, CI = 46, RI = 67). The strict consensus of those trees (Fig. 20a; L = 144, CI = 40, RI = 57) caused the collapse of 10 nodes. As in the phylogenetic analysis of all Epeolini, Old World and New World *Triepeolus* form a monophyletic group. Unlike the first analysis, *Thalestria* is sister to *Doeringiella*. The analysis that employed all *Epeolus* except those included in *Trophocleptria* (sensu Michener, 2000; see Table 3), produced 70 equally parsimonious trees (L = 191, CI = 47, RI = 71). The strict consensus caused 7 nodes to collapse (Fig. 20b; L = 203, CI = 44, RI = 71). *Thalestria* is again sister to *Doeringiella*; however the two are sister to New World *Triepeolus*. The two Old World *Triepeolus* species form a clade that, in turn, forms an intuitively unlikely pairing with *Rhinepeolus* and *Pseudepeolus*. Finally, 585 equally parsimonious trees were found in the analysis that employed all *Epeolus* species listed in Table 3 as the outgroup to Thalestriina (L = 208, CI = 47, RI = 76). The strict consensus of these trees collapsed

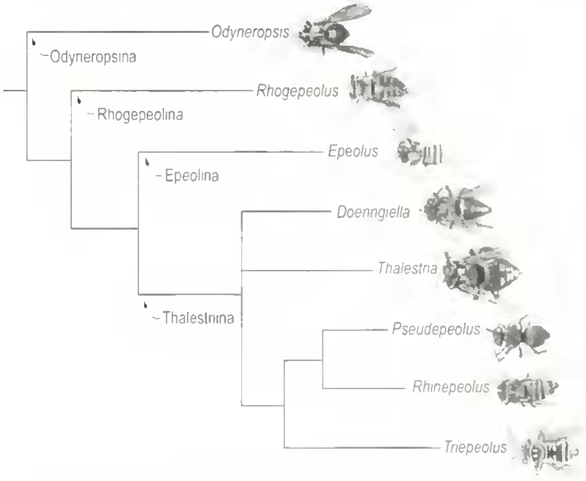
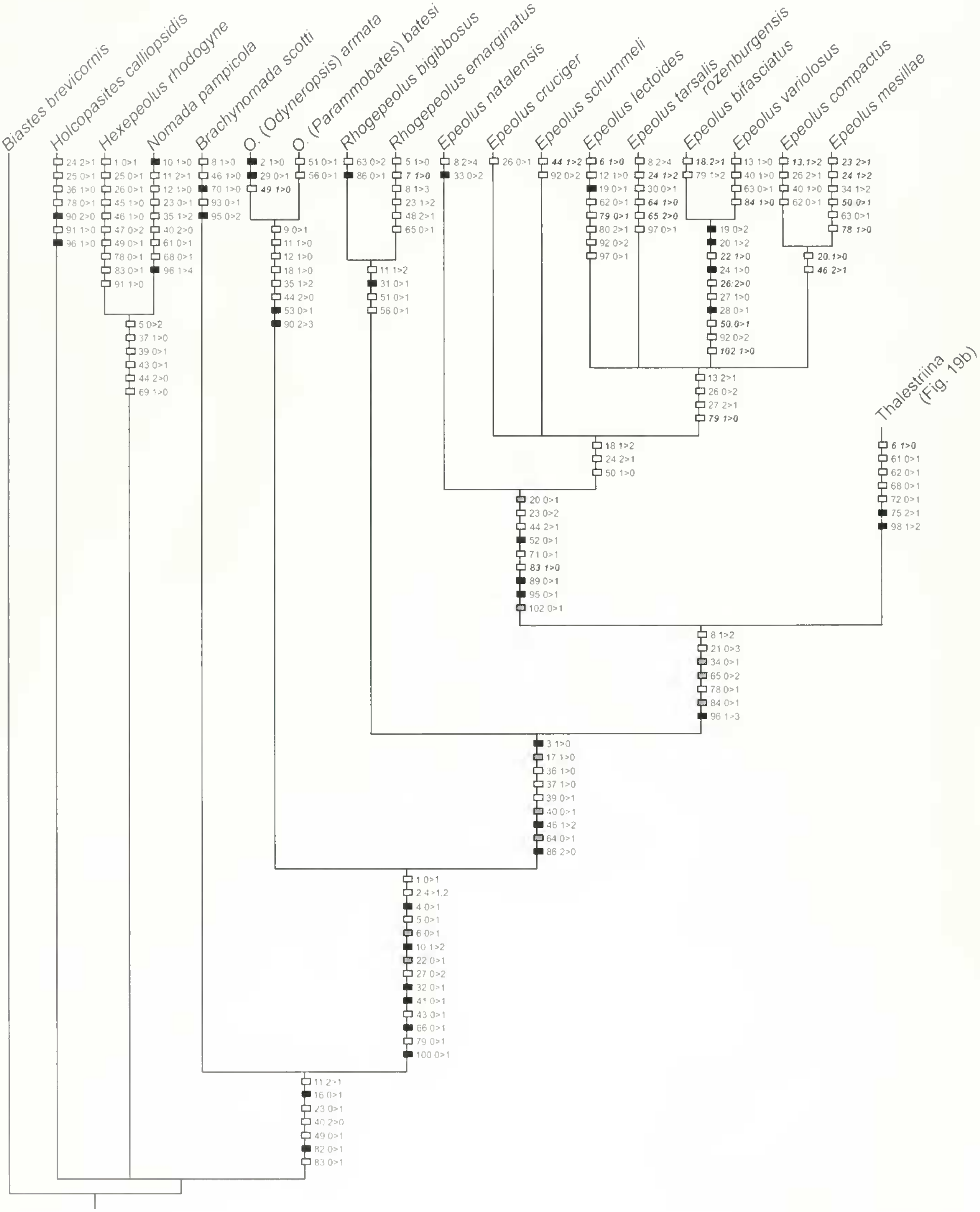
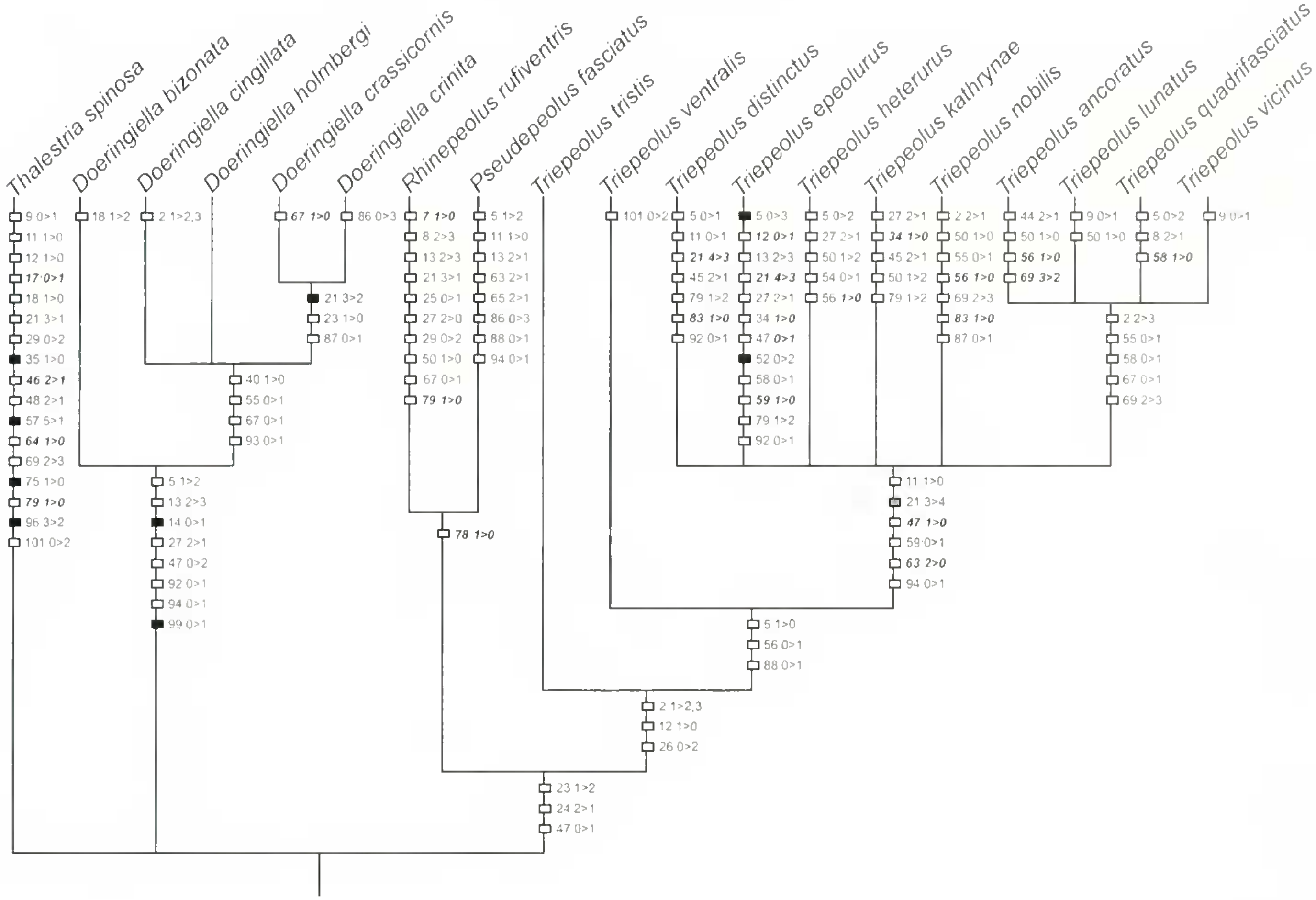


Fig. 18. Summary of phylogenetic relationships of epeoline genera presented in Fig. 19. Images right of genus names are, from top to bottom, *Odyneropsis* (*Parammobates*) *batesi*, *Rhogepeolus bigibbosus*, *Epeolus mesillae*, *Doeringiella bizonata*, *Thalestria spinosa*, *Pseudepeolus fasciatus*, *Rhinepeolus rufiventris*, and *Triepeolus kathrynae*.


Biastes brevicornis
Holcopasites calliopsidis
Hexepeolus rhodogyne
Nomada pampicola
Brachynomada scotti
O. (Odyneropsis) armata
O. (Parammobates) batesi
Rhogepeolus bigibbosus
Rhogepeolus emarginatus
Epeolus natalensis
Epeolus cruciger
Epeolus schummeli
Epeolus lectoides
Epeolus tarsalis
rozenburgensis
Epeolus bifasciatus
Epeolus variolosus
Epeolus compactus
Epeolus mesillae
Thalestriina (Fig. 19b)
24 2>1
25 0>1
36 1>0
78 0>1
90 2>0
91 1>0
96 1>0
1 0>1
25 0>1
26 0>1
45 1>0
46 1>0
47 0>2
49 0>1
78 0>1
83 0>1
91 1>0
10 1>0
11 2>1
12 1>0
23 0>1
35 1>2
40 2>0
61 0>1
68 0>1
96 1>4
5 0>2
37 1>0
39 0>1
43 0>1
44 2>0
69 1>0
8 1>0
46 1>0
70 1>0
93 0>1
95 0>2
2 1>0
29 0>1
49 1>0
51 0>1
56 0>1
9 0>1
11 1>0
12 1>0
18 1>0
35 1>2
44 2>0
53 0>1
90 2>3
63 0>2
86 0>1
5 1>0
7 1>0
8 1>3
23 1>2
48 2>1
65 0>1
11 1>2
31 0>1
51 0>1
56 0>1
8 2>4
33 0>2
26 0>1
44 1>2
92 0>2
6 1>0
12 1>0
19 0>1
62 0>1
79 0>1
80 2>1
92 0>2
97 0>1
8 2>4
24 1>2
30 0>1
64 1>0
65 2>0
97 0>1
18 2>1
79 1>2
13 1>0
40 1>0
63 0>1
84 1>0
13 1>2
26 2>1
40 1>0
62 0>1
23 2>1
24 1>2
34 1>2
50 0>1
63 0>1
78 1>0
19 0>2
20 1>2
22 1>0
24 1>0
26 2>0
27 1>0
28 0>1
50 0>1
92 0>2
102 1>0
20 1>0
46 2>1
13 2>1
26 0>2
27 2>1
79 1>0
18 1>2
24 2>1
50 1>0
20 0>1
23 0>2
44 2>1
52 0>1
71 0>1
83 1>0
89 0>1
95 0>1
102 0>1
6 1>0
61 0>1
62 0>1
68 0>1
72 0>1
75 2>1
98 1>2
8 1>2
21 0>3
34 0>1
65 0>2
78 0>1
84 0>1
96 1>3
3 1>0
17 1>0
36 1>0
37 1>0
39 0>1
40 0>1
46 1>2
64 0>1
86 2>0
1 0>1
2 4>1,2
4 0>1
5 0>1
6 0>1
10 1>2
22 0>1
27 0>2
32 0>1
41 0>1
43 0>1
66 0>1
79 0>1
100 0>1
11 2>1
16 0>1
23 0>1
40 2>0
49 0>1
82 0>1
83 0>1



Figs. 19a (left) and b (above). Topology of the strict consensus of 396 most parsimonious trees (L = 404, CI = 41, RI = 71) based on 102 morphological characters (Thalestriina shown in Fig. 19b). The character list and data matrix are found in Appendices 2 and 3, respectively. Black bars represent unique, unreversed transformations; gray bars are unique transformations that are reversed on more terminal nodes; white bars are transformations that appear more than once on the tree. Numbers left of the colons refer to character number; numbers right of the colons indicate the character-state transformation. Characters in bold-faced italics are reversals.

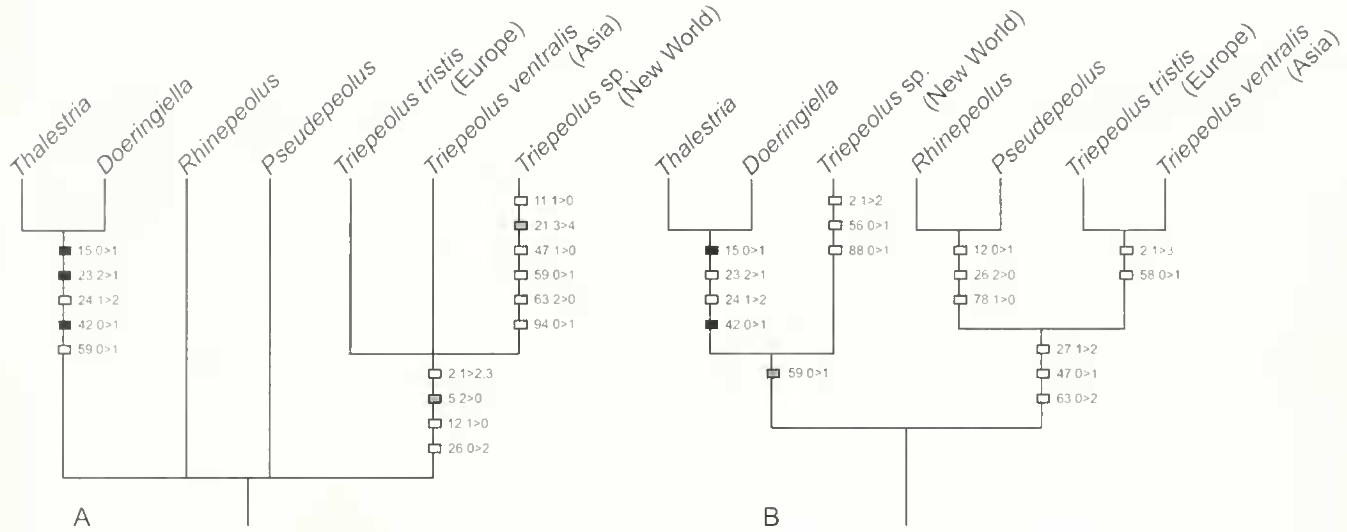
19 nodes, producing an almost complete polytomy (L = 266, CI = 36, RI = 63). The only resolved clade was a monophyletic *Doeringiella*; no *Triepeolus* species grouped together, and none of the other taxa (each represented by only one species) formed sister-group pairings.

Because of these results, no attempt is made herein to draw conclusions about the relationships among the thalestriine genera. However, pertinent characters that suggest various relationships among the genera are discussed below.

SYSTEMATICS

TRIBE EPEOLINI ROBERTSON

Diagnosis.—Epeolines are characterized by the presence of the following synapomorphies: the two apical or subapical tubercles on the labrum, 4(1) (Figs. 34, 35, and 37; not considered homologous with the apical fringe of irregular tubercles in *Nomada*); the presence of a subapical mandibular tooth formed by the trimmal extension, 6(1) (lost in Thalestriina); the lateroclypeal carina, which forms an almost continuous carina with the paraocular carina, 10(2) (Fig. 39); the dorsal surface of the pronotum, which is convex along the anterior margin, 22(1) [reversed in *Epeolus* (*Trophocleptria*), sensu Michener, 2000]; the axillar spines, which are sometimes very small, 32(1); the roughly quadrate procoxa and widely separated trochanters, 41(1); the elongate and broadly trough-shaped female S5, 66(1); and the inner, medial projection of the penis valve, 100(1) (Figs. 128A and 131–138). The tribe is also characterized by the sclerotized galea, 1(1) (also in *Hexepeolus*), and the



Figs. 20a and b. Phylogenetic analyses of Thalestriina. Where applicable, clades represented by several species in the analyses are shown collapsed as a single branch. Only those characters supporting relationships between two or more clades are shown. Black bars represent unique, unreversed transformations; gray bars are unique transformations that are reversed on more terminal nodes; white bars are transformations that appear more than once on the tree. Numbers left of the colons refer to character number; numbers right of the colons indicate the character-state transformation. a. Strict consensus of 90 most parsimonious trees (L = 144, CI = 40, RI = 57) using only *Epeolus natalensis* as the outgroup. b. Strict consensus of 70 most parsimonious trees (L = 203, CI = 44, RI = 71) using all *Epeolus* listed in Table 3 except for *Epeolus bifasciatus* and *Epeolus variolosus* (i.e., those *Epeolus* belonging to *Trophocleptria*, sensu Michener, 2000). See Phylogenetic Results for further explanation.

patch of dense setae on the anterior margin of the outer mesotibia, 43(1) (Fig. 172; also in *Hexepeolus* and *Nomada*, although the lack of these setae in *Holcopasites*, *Biastes*, and *Brachynomada* may be linked to the smaller size of those bees). Additionally, according to Roig-Alsina and Michener (1993), epeolines are characterized by the shallow postoccipital pouch below the foramen magnum and several characters of the mouthparts: the absence of a glossal rod, the relatively wide, internal sclerotized surface of the galeal blade, the absence of a longitudinal row of bristles on the anterior internal surface of the maxillary galea, and the membranous inner margin of the first labial palpal segment.

Comments.—The presence of only two maxillary palpal segments (the distal palpal segment short or elongate), 2(1,2), was resolved as the plesiomorphic condition for the tribe. This seems less likely than Alexander's (1990) finding that three maxillary palpal segments is plesiomorphic, since the loss may be more likely than the gain of a segment. However, it may be that considerable sub-segmentation or fusion between segments has occurred, given the observation of three small segments on one side and one small segment and one elongate segment on the other side of the same individual of some taxa. The presence of a digitiform appendage on the basal apodeme of the female S6, 79(1), was also resolved as plesiomorphic to Epeolini.

SUBTRIBE ODYNEROPSINA HANDLIRSCH, NEW STATUS

Odyneropsini Handlirsch, 1925:821. Type genus: *Odyneropsis* Schrottky, 1902

Diagnosis.—This subtribe consists of bees that resemble polistine wasps and lack the bands of appressed setae that characterize most epeolines. Characters supporting this clade are the relatively long pterostigma, 35(2) (Fig. 51); the globular, deeply rugoso-striate setae on the pseudopygidial area, 53(1) (Fig. 180B); and the long, rounded lateral apodemes of the male S8, 90(3) (Figs. 98 and 99). The subtribe is also characterized by the median clypeal carina, 9(1); the relatively short F1 (less than or equal to 0.75 F2), 11(0); the antennal pedicel of males, which are set into the apex of the scape, 12(0); the interocellar distance, which approximately equals the width of the lateral ocellus, 18(0); and the absence of thick, spine-like setae on the posterior-facing surface of the mesotibia, 44(0).

Comments.—This is the basalmost subtribe within Epeolini.

GENUS *ODYNEROPSIS* SCHROTTKY

Diagnosis.—See Odyneropsina (above).

Comments.—The similarity of certain characters of *Odyneropsis* and *Rhogepeolus*, especially the male genitalia and the female pseudopygidial area and S6, has been noticed by several authors (e.g., Moure 1955, Roig-Alsina 1996). Alexander's (1990) phylogeny, which excluded characters of the female S6, resolved *Odyneropsis* and *Rhogepeolus* as a clade. Michener (2000) hypothesized that *Odyneropsis* might be derived from a *Rhogepeolus*-like ancestor. Indeed, there are several characters that would suggest a sister-group relationship between *Odyneropsis* and

Rhogepeolus, but which may simply be the plesiomorphic condition for the tribe as a whole (as the present phylogeny would indicate). They include the elongate sclerotized disk of the female S6, 68(0), with the digitiform appendage of the basal apodeme attached sub-basally, widely mesal to the main body of the basal apodeme, 80(0) (Figs. 11 and 12); the dense regions of branched setae on the lateral margins of the male S7, 87(2) (Figs. 64–67; minute branching not indicated for *Odyneropsis*); and the dorsal connecting bridge of the penis valves, which is expanded into a spatha, 96(1). The medioapical slit of the pseudopygidial area, 51(1) (not always present in *Odyneropsis*; Figs. 179A and 181), is unique to these genera and might represent a true synapomorphy, although it is here resolved as convergent.

SUBGENUS *ODYNEROPSIS* SCHROTTKY, NEW STATUS

Odyneropsis Schrottky, 1902:432. Type species: *Odyneropsis holosericea* Schrottky, 1902 [= *Rhathymus armatus* Friese, 1900:65], by original designation.

Diagnosis.—I have not been able to examine all described species of *Odyneropsis*; however, the apparent synapomorphy of this subgenus is the mid-dorsal depression of the female T5, which is entirely or almost entirely bordered by carinae (Fig. 180A). This character appears to be correlated with larger body size (about 14 mm or more). *Odyneropsis* (*Odyneropsis*) *armata* differs from *Odyneropsis* (*Parammobates*) *batesi* by having only one maxillary palpal segment, 2(0) [although Moure (1955) described a female of *O. armata* that had two maxillary palpal segments on one side]; the scutellum, which bears mammiform tubercles, 29(1); the extremely long hind tibia (5 times longer than wide, as opposed to 4 times longer than wide); and the presence of robust setae on the ventral margin of the gonostylus (Fig. 131).

Comments.—Based on personal examination and the original descriptions, the following species are likely to be included in this subgenus: *Odyneropsis apache* Griswold and Parker[4], *O. apicalis* Ducke, *O. armata* Friese, *O. foveata* (Ducke), *O. gertschi* Michener, *O. pallidipennis* Moure, and *O. vespiformis* (Ducke).

SUBGENUS *PARAMMOBATES* FRIESE, NEW STATUS

Parammobates Friese, 1906:118. Type species: *Parammobates brasiliensis* Friese, 1906, monobasic.

Diagnosis.—This subgenus differs from *Odyneropsis* sensu stricto by the smaller size (11 mm or less) and the incomplete mid-dorsal depression of the female T5, which is not anteriorly bordered by a carina or differentiated setae (Fig. 181). *Odyneropsis* (*Parammobates*) *batesi* differs from *O.* (*Odyneropsis*) *armata* by the presence of two maxillary palpal segments, 2(1); the sclerotized plates medially on the penis (Fig. 139); and the dense area of simple setae on the posterolateral angle of the female metatibia (similar to those of Epeolina and Thalestriina), 45(2).

Comments.—*Odyneropsis* (*Parammobates*) *batesi* bears a medioapical slit on the apical margin of the pseudopygidial area; however, this slit is not a consistent feature of *Parammobates* as it is absent in *Odyneropsis* (*Parammobates*) *brasiliensis*, the type species of *Parammobates*. The following species are likely to be included in this subgenus: *Odyneropsis batesi* Cockerell, *O. brasiliensis* (Friese), *O. columbiana* Schrottky, and *O. melancholica* Schrottky.

RHOGEPEOLINA, NEW SUBTRIBE

Type genus: *Rhogepeolus* Moure, 1955.

Diagnosis.—The only synapomorphy recovered by the present phylogeny to unite this subtribe is the distinct median longitudinal strip of appressed setae between the convexities of the scutellum, 31(1). This character is weakened by the presence of similar but less complete bands in a few species of *Doeringiella* and *Triepeolus*. Nonetheless, a number of characteristics make this group easy to recognize. The pseudopygidial area is particularly distinctive, with a strongly concave apical margin, 50(2), bearing a medioapical slit, 51(1). The lateral margins of this slit and the apical margin of the pseudopygidial area are fringed with relatively long, curved, simple setae (Fig. 179). The pseudopygidial area is located on a posterior facing plane of T5, with short, simple setae that are curved towards the midline. In addition, the female mesotibia and metatibia bear rounded, stout spines along their apical margins, 45(1) (Figs. 172 and 173); the female pygidial plate has a glabrous, median longitudinal ridge, 56(1); and the male S7 is characterized by a dense region of long, branched setae on the lateral margins of the distal process, 87(2) (Figs. 64 and 65).

GENUS *RHOGEPEOLUS* MOURE

Rhogepeolus Moure, 1955:117. Type species: *Rhogepeolus bigibbosus* Moure, 1955, by original designation.

Coptepeolus Moure, 1955:120. Type species: *Coptepeolus emarginatus* Moure, 1955, by original designation.

Diagnosis.—See Rhogepeolina (above).

Comments.—*Rhogepeolus* contains a spectrum of relatively divergent morphological forms, with *Rhogepeolus emarginatus* and *Rhogepeolus bigibbosus* representing the extremes. The fact that Moure (1955) originally placed these two species in separate genera is indicative of the extent of their differences; however, Roig-Alsina (1996) discovered additional species that caused these morphological differences to intergrade. According to Alexander (1990), the apex of the marginal cell is truncated or oblique in this genus, but I found this difficult to distinguish from the rounded state found in other epeolines. The genus presently consists of five species, all from South America (Roig-Alsina, 1996; Rightmyer, 2003).

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[4] Based on the original description, this species is likely the same as the putative "new genus" among the material from Arizona observed by Brumley (1965: 5–6).

Rhogepeolina + (Epeolina + Thalestriina)

Comments.—Several synapomorphies support the sister-group relationship of Rhogepeolina to all other Epeolini excluding Odyneropsina. The synapomorphies are the contact of both mandibular articulations with the compound eye, 3(0); the ventrally convergent compound eyes of males, 17(0) (parallel in *Thalestria*); the relatively short second abscissa of hindwing vein M+Cu, 40(1) (relatively long in most *Doeringiella*); the dorsally enlarged bases of the spine-like setae of the metatibia, 46(2) (Fig. 174); the elongate, curved apical setae of the male S4, 64(1) (not elongate in *Thalestria*); and the roughly straight, parallel sided lateral margins of the male S7, 86(0) (rounded in some Thalestriina). These subtribes are also characterized by the forewing vein r-rs, which arises from point distal to the midpoint of the pterostigma, 36(0) (Figs. 52 and 53); the length of all the submarginal cells together, which is distinctly greater than the length of marginal cell, 37(0); and the papilliform setae on the forewing distal to the closed cells 39(1).

Epeolina + Thalestriina

Comments.—The synapomorphies supporting the sister-group relationship of the subtribes Epeolina and Thalestriina are: the forewing radial cell with the setae primarily restricted to the upper (i.e., costal) half or less of the cell, 34(1) (more or less dense in a minority of taxa); the elongate, curved setae of the male S5, 65(2) (less pronounced in *Pseudepeolus*); the apical, sublateral emarginations of the male S7, 84(1) (Figs. 68–95); and the roughly bar shaped dorsal connecting bridge of the penis valves, 96(3) (triangular in *Thalestria*; reduced in some *Epeolus*). This clade is also characterized by the roughly pentagonal-shaped swelling of the supraclypeal area, 8(2); the absence of the preoccipital carina on the upper corners of the head, 21(3) (Fig. 32); the strongly sclerotized V or U shape formed by the inner and outer margins of the female S6 near the mediolateral apodeme, 78(1) (Figs. 7, 9, 10, and 13); and the position of the lateral sulcus of the male gonocoxite, which runs obliquely from the base of the gonostylus to a more ventral and basal position on the gonocoxite (see arrow, Fig. 133).

Subtribe Epeolina Robertson, new status

Epeolinae Robertson, 1903:284. Type genus: *Epeolus* Latreille, 1802.

Diagnosis.—Epeolina can be distinguished from other Epeolini by the following synapomorphies: the dorsal protrusion of the gena, 20(1) [Figs. 41 and 42; enlarged in *Trophocleptria*, sensu Michener, 2000]; the silvery band of apically rounded, flattened setae on the pseudopygidial area, 52(1) (Figs. 190 and 191); the principal setae at the apex of the female S6, which forms conical denticles, 70(2) (Fig. 13); the dorsoapical setae on the lateral lobes of the male S7, 89(1) (Figs. 68–76); the single, elongate gonostylus that is angled basally into a lobe, 95(1) (Fig. 129); and the widely divergent lobe on the dorsolateral margin of the penis, 102(1) (Fig. 141) [absent in *Trophocleptria*, sensu Michener, 2000; Fig. 142]. The subtribe is additionally characterized by the relatively long, dorsal posterior surface of the pronotum (about equal to median ocellar diameter), 23(2); the relatively few, scattered spine-like setae on posterior-facing surface of the mesotibia, 44(1); and the lack of a median emargination at the apex of the male S7, 83(0). The subtribe can additionally be distinguished from most Thalestriina by the relatively more apical position of the lateral lobes to the interlobal area of the male S7, 85(0).

Genus *Epeolus* Latreille

Epeolus Latreille, 1802:427. Type species: *Apis variegata* Linnaeus, 1758, monobasic.

Trophocleptria Holmberg, 1886c:275. Type species: *Trophocleptria variolosa* Holmberg, 1886c, monobasic. [new synonymy]

Epeolus (*Diepeolus*) Gribodo, 1894:79. Type species: *Epeolus giannellii* Gribodo, 1894, monobasic.

Epeolus (*Monoepeolus*) Gribodo, 1894:80. Type species: *Apis variegata* Linnaeus, 1758, by original designation.

Pyrrhomelecta Ashmead, 1899:66. Type species: *Epeolus glabratus* Cresson, 1878, by original designation.

Argyroselenis Robertson, 1903:284. Type species: *Triepeolus minimus* Robertson, 1902, by original designation.

Oxybiastes Mavromoustakis, 1854:260. Type species: *Oxybiastes bischoffi* Mavromoustakis, 1954, by original designation.

Diagnosis.—See Epeolina (above).

Comments.—Diagnostic characteristics of at least some *Epeolus* were discovered by Roig-Alsina and Michener (1993). They include the well developed, fan shaped posterior sheets of the tentorium, the posteriorly curved pre-episternal internal ridge, and absence of the lower extremity of the metapostnotum.

Michener (2000) recognized *Trophocleptria* as a subgenus of *Epeolus*. *Trophocleptria* is a distinctive group; however, it renders *Epeolus* sensu stricto paraphyletic. A species-level analysis of the entire genus *Epeolus* will likely resolve clades that will allow for the recognition of *Trophocleptria* along with several other new genera or subgenera of *Epeolus*. The monophyly of *Trophocleptria* seems likely to remain stable, given the number of synapomorphies uniting *Epeolus bifasciatus* (a geographical outlier from North America that is generally considered intermediate between *Epeolus* sensu stricto and *Trophocleptria*; Michener, 2000) with *Epeolus variolosus*, including the pronounced dorsal genal protrusion, 20(2), and the waxy, glabrous lobe between the compound eye and lateral ocellus, 19(2) (Fig. 42); the position of the dorsal posterior surface of the pronotum near the dorsal surface of the scutum, 24(0) (Fig. 50); the carinate or flattened projections of the deeply areolate scutellum, 28(1); and the absence of the widely divergent lobe on the dorsolateral margin of the penis that characterizes all other examined *Epeolus*, 102(0).

THALESTRIINA, NEW SUBTRIBE

Type Genus: *Thalestria* Smith, 1854.

Diagnosis.—The subtribe Thalestriina is primarily characterized by the female S6: the principal setae are elongate, pointed, and hooked, 70(3); the sclerotized disk is reduced (sometimes extremely reduced to a rod-like connection between the apical processes of the S6), 68(1); and the mediolateral apodeme is relatively basal on the S6 (i.e., the length of the female S6 basal to the mediolateral apodeme equals 30–40% of the total S6 length or less), 75(1) (Figs. 7, 9, 10, and 22B). Additionally, the female S6 lacks marginal setae medially between the apical processes, 72(1), and the apical process has a flat, stake-like, usually three pronged apical plate dividing the principal setae from the dorsoapical setae, 73(2). An additional synapomorphy is the dorsobasal lobe of the penis valve, which conspicuously covers the basolateral margins of the penis, 98(2). Other characterizations of the subtribe are the absence of a distinct subapical mandibular tooth, 6(0); the apodemal region of the female T7, which roughly forms a right angle, 61(1) (Figs. 160–165); and the cross bar that extends from the anterior ridge of the female T8, 62(1) (Figs. 150 and 151). All Thalestriina except *Thalestria* are additionally characterized by the lateral, scroll-like processes found on the apical ventral surface of the female pygidial plate, 57(5) (Fig. 178)

GENUS *THALESTRIA* SMITH

Thalestria Smith, 1854:283. Type species: *Thalestria smaragdina* Smith, 1854 [= *Euglossa spinosa* Fabricius, 1804:362], monobasic.

Diagnosis.—*Thalestria* is immediately distinguishable from all other epeolines by the bright metallic blue and green scales that clothe the majority of the body. The pterostigma is relatively small (1.5 times the prestigma length). 35(0) (Fig. 52); the apical ventral surface of female pygidial plate, in posterior view, forms one median, rounded process, 57(1) (Fig. 175); the lateral process of the female T7 is dramatically elongate, 59(2) (Fig. 162); the mediolateral apodeme is extremely basal in its location along the lateral margin of the female S6 (i.e., the length of the female S6 basal to the mediolateral apodeme is only 15% of total S6 length), 75(0) (Fig. 10); and the dorsal connecting bridge of penis valves is roughly triangular, 96(2). Additional distinctive traits of the genus are the position of the preoccipital carina much below the ocelli on the posterior surface of the head; the two plate-like integumental structures that meet at an angle along an impressed line on the vertex behind the median ocellus; and the relatively large eyes (especially of males). *Thalestria* is additionally characterized by the parallel compound eyes of the males, 17(1); the relatively small interocellar distance, 18(0); the continuous preoccipital carina, which lacks angles at the upper corners of the head, 21(1); the enlarged mammiform tubercles on the scutellum, 29(2); the unmodified (i.e., not dorsally enlarged) bases of the metatibial spine-like setae, 46(1); the restriction of the appressed setae to small spots on the metasoma, 48(1); the lack of elongate or curved setae at the apex of the male S4, 64(0); the straight, bar shaped disk that is roughly perpendicular to the inner margins of the apical processes of the female S6, 69(3); the lack of a digitiform appendage on the basal apodeme of the female S6, 79(0); and the male S7, which has the lateral margins of the distal plate above the interlobal area, 85(0).

Comments.—The relationship of *Thalestria* to the other genera of Thalestriina is poorly resolved in the phylogenetic analysis of Epeolini (Fig. 19b). Two of the restricted phylogenies of Thalestriina (Fig. 20) placed *Thalestria* as the sister taxon to *Doeringiella* based on the prominent depression of the frons behind the scape, 15(1); the relatively short dorsal posterior surface of the pronotum (much less than an ocellar diameter), 23(1); and the long setae on underside of male mesofemur, 42(1). They also share the arching anterior surface of the scutum, 24(2).

Alternatively, *Thalestria* and *Rhinepeolus* share the continuous preoccipital carina that does not form angles at the upper corners of the head, 21(1); the enlarged mammiform tubercles of the scutellum, 29(2); and the lack of a digitiform appendage on the basal apodeme of the female S6, 79(0).

Thalestria shares with New World *Triepeolus* the short female F1 relative to F2, 11(0), as well as the absence of elongate, curved setae at the apex of the male S3, 63(0). The straight, bar shaped disk that is roughly perpendicular to the inner margins of the apical processes of the female S6, 69(3), is shared by *Thalestria* and some New World *Triepeolus*, suggesting the possibility that *Thalestria* is derived from within *Triepeolus*. The extremely elongate lateral process of the female T7, 59(2), would similarly seem to be a continued derivation of the elongate lateral process found in *Doeringiella* and New World *Triepeolus* (except *Triepeolus epeolurus*), 59(1). New World *Triepeolus* (except *T. epeolurus*) also share with *Thalestria* the complete lack of a basitibial plate, 47(0) (a partial basitibial plate being found in Old World *Triepeolus*, *T. epeolurus*, *Rhinepeolus*, and most *Pseudepeolus*, and a complete basitibial plate being found in *Doeringiella*, *Pseudepeolus willinki*, and *Pseudepeolus carinata*, according to Roig-Alsina, 2003).

Support for the basal position of *Thalestria* within Thalestriina may come from Alexander's (1990) coding that it shares with *Epeolus*, *Rhogepeolus*, and *Odyneropsis* the presence of an inner dorsal carina or lamella on the metacoxa, which is lacking in *Triepeolus*, *Doeringiella*, and *Rhinepeolus*. While there is a tendency for these latter groups to have a weaker, shorter carina than other members of the Epeolini, the character is not consistent. For example, some *Triepeo-*

lus (e.g., *Triepeolus ancoratus*) possess a strong inner dorsal lamella on the metacoxa.

Genus *Doeringiella* Holmberg

Doeringiella Holmberg, 1886a:151. Type species: *Doeringiella bizonata* Holmberg, 1886a, monobasic.

Doeringiella (*Orfilana*) Moure, 1954:266. Type species: *Doeringiella variegata* Holmberg, 1886c [=*Epeolus holmbergi* Schrotty, 1913:265], by original designation.

Diagnosis.—The monophyly of *Doeringiella* is supported by the male and female scape, which, when not swollen, bears a sub-basal angle on the plical surface, 14(1), and the highly recurved, scroll-like articulating surfaces of the penis valve, 99(1). Both characters are further discussed and clarified by Roig-Alsina (1989). The genus is additionally characterized by the depressed regions of the frons behind the scape, 15(1) (Fig. 167); the relatively long scape (i.e., greater than two times the width of the scape), 13(3); the weak biconvexities of the scutellum, 27(1); the long setae on the underside of the male mesofemur (not in *Doeringiella chacoensis*; Roig-Alsina, 1989), 42(1); the completely bordered basitibial plate (both sexes), 47(2); the medially emarginate sides of the medioapical process of the male S8, 92(1) (Figs. 114–118; however, they are not emarginate in *Doeringiella arechavaletai, D. paranensis, D. gigas*, and *D. cochabambina*, according to Roig-Alsina, 1989); and the distinctly emarginate ventral margin of the male gonocoxite, 94(1) (Fig. 136). Furthermore, there is a tendency for a narrowing of sclerotized areas basally on the penis valves (Fig. 145). Most conspicuously, males of several species of this genus bear dramatically swollen scapes.

Comments.—*Doeringiella, Triepeolus*, and *Pseudepeolus* were given subgeneric status under the genus *Doeringiella* by Michener (2000). This decision was largely due to similar characteristics of the male genitalia, especially the emarginate male gonocoxite, 94(1), and the elongate, bar shaped dorsal connecting bridge of the penis valves, 96(3). Support for this classification is weakened by the findings that the bar shaped dorsal connecting bridge of *Pseudepeolus* is similar to that found in *Rhinepeolus*, and that the emarginate male gonocoxite is not possessed by Old World *Triepeolus*. Nonetheless, species of *Doeringiella* share the emarginate ventral margin of the male gonocoxite with *Pseudepeolus* and New World *Triepeolus*; they also share the elongate lateral process of the female T7 with all New World *Triepeolus* except *Triepeolus epeolurus*. Alternatively, *Doeringiella* shares with Old World *Triepeolus* and *Rhinepeolus* the presence of elongate, curved setae on the apical margin of the male S3, 63(2); it shares with *Rhinepeolus* and *T. epeolurus* the relatively long scape, 13(3).

The relationships of the *Doeringiella* species resolved by the present phylogenetic study do not correspond well with those recovered by Roig-Alsina (1989) or Compagnucci and Roig-Alsina (2003), whose phylogenies were specifically constructed to address the internal relationships of that genus. The incongruence might be explained by the fact that the present study did not include all species of *Doeringiella*, nor did it include all pertinent characters related to the genus.

Genus *Rhinepeolus* Moure

Rhinepeolus Moure, 1955:115. Type species: *Epeolus rufiventris* Friese, 1908, by original designation.

Diagnosis.—*Rhinepeolus* is most readily differentiated from all other Epeolini by the form of the female pseudopygidial area, which has a median, longitudinal region of stout, simple setae that give the impression of a furrow (Fig. 183). The mesocoxa of this genus has a distinct, prominent carina present between the anterior and posterior coxotrochanteral articulations; also, the female T6 bears a flange lateral to the pygidial plate that is absent in all other Epeolini. It is distinct from other Thalestriina by the exceptionally bulbous protrusion of the supraclypeal area, 8(3), which bears a weakly carinate frontal line, 7(0) (Fig. 168); the presence of a median longitudinal band of appressed setae on the scutum, 25(1); the absence of biconvexity, 27(0), coupled with the presence of enlarged mammiform tubercles on the scutellum, 29(2) (such tubercles also found in *Thalestria*); and the sparsely scattered setae on the forewing radial cell, 34(2). The genus is additionally characterized by the concave apical margin of the labrum, 5(1); the relatively long, slender scape, 13(3); the continuous, smoothly rounded preoccipital carina, 21(1); the presence of a basitibial plate that is incompletely bordered by a carina, 47(1); the poorly defined metapostnotum; the relatively long second abscissa of the hindwing vein M+Cu (over twice as long as cu-a), 40(0); the convex apical margin of the pseudopygidial area, 50(0); the apical, ventrally directed lip of the female S5, 67(1); the absence of a distinctly sclerotized connection between the inner and outer margins of the female S6 near the mediolateral apodeme, 78(0); and the lack of a digitiform appendage on the basal apodeme of the female S6, 79(0).

Comments.—A sister-group relationship of *Rhinepeolus* to *Pseudepeolus* was recovered in the phylogenetic analysis of all Epeolini, supported only by the appearance of the inner basal margin of the female S6, which does not conspicuously meet the outer margin near the mediolateral apodeme, 78(0). *Rhinepeolus* shares the apical, ventrally directed lip of the female S5 with several species of *Triepeolus* and *Doeringiella*, 67(1). Other characters that could potentially support the relationship of *Rhinepeolus* with other thalestriine genera are discussed in the Comments sections of *Thalestria* and *Doeringiella*.

Genus *Pseudepeolus* Holmberg

Pseudepeolus Holmberg, 1886c:284. Type species: *Pseudepeolus fasciatus* Holmberg, 1886c, monobasic.
Pseudopeolus Ashmead, 1899:80. *Lapsus calami.*
Doeringiella (*Stenothisa*) Moure, 1954:277. Type species: *Doeringiella angustata* Moure, 1954, by original designation.

Diagnosis.—Superficially, species of *Pseudepeolus* most resemble *Doeringiella*, especially in the overall appearance of the pseudopygidial area. Unfortunately, I was unable to study specimens of basal *Pseudepeolus* species (e.g., *Pseudepeolus willinki* or *P. carinata*), as resolved by Roig-Alsina (2003). Based on observations of *Pseudepeolus fasciatus* (and, to a more limited degree, a male specimen of *Pseudepeolus angustata*), the genus can be distinguished from other Thalestriina by the relatively short scape (about 1.5 longer than width), 13(1), which is flattened in the male, and the dense setae on the forewing radial cell, 34(0). *Pseudepeolus* is characterized by the apical margin of labrum, which bears a process, 5(2) (Fig. 37; considered to be a third apical tubercle by Roig-Alsina, 2003); the relatively short female F1 compared to F2, 11(0); the presence of a basitibial plate that is incompletely bordered by a carina, 47(1) (entirely bordered in *P. willinki* and *P. carinata*; Roig-Alsina, 2003); the straight, elongate setae at the apex of the male S3, 63(1), and S5, 65(1) (apical fringe of S3 more developed in *P. willinki*; Roig-Alsina, 2003); the male S7 with rounded lateral margins of the distal plate, 86(3) (Fig. 79); and the emarginate ventral margin of the male gonocoxite, 94(1) (Fig. 137). While the pseudopygidial area of this genus superficially resembles that of *Doeringiella*, scanning electron microscopy has revealed a number of setal types that are presently unique to *P. fasciatus*, if not all *Pseudepeolus*. Especially striking are the sharply pointed setae that fringe the apical margin of the pseudopygidial area (Fig. 184B).

Comments.—Roig-Alsina (2003) used the dorsal separation of the preoccipital carina from the compound eye margin as a synapomorphy for *Pseudepeolus*; however, I found this character difficult to use since the preoccipital carina disappears at the upper corner of the head in many Thalestriina. For discussion of the characters that might support a relationship of *Pseudepeolus* with other thalestrine genera, refer to the Comments sections of *Thalestria*, *Doeringiella*, and *Rhinepeolus*.

Genus *Triepeolus* Robertson

Triepeolus Robertson, 1901:231. Type species: *Epeolus concavus* Cresson, 1878, by original designation.
Triepeolus (*Synepeolus*) Cockerell, 1921:6. Type species: *Triepeolus insolitus* Cockerell, 1921, monobasic.
Triepeorus Tadauchi and Schwarz, 1999:47. *Lapsus calami.*

Diagnosis.—The dearth of synapomorphic characters supporting the monophyly of *Triepeolus* is indicative of the range of morphological variation within this group. The most consistent character separating members of *Triepeolus* from other Thalestriina would seem to be the presence of two longitudinal bands of appressed setae that extend roughly to the middle of the scutum, 26(2); however, these bands are not present on all *Triepeolus* species [e.g., *Triepeolus mexicanus* (Cresson)]. The genus is additionally characterized by the presence of three or two maxillary palpal segments (with the distal segment elongate, except in *Triepeolus nobilis* where it is small), 2(2,3); the antennal pedicel of males, which is set into the apex of the scape, 12(0) (more fully exposed in *Triepeolus epeolurus*); and the distinct pocket of setae found in the apical emargination near the lateral lobe on the ventral surface of the male S7, 88(1) (Figs. 86–95; pocket of setae not distinct in *Triepeolus tristis*). Additionally, the dorsal surfaces of the penis valves tend to be more sclerotized in *Triepeolus* than in other epeolines (Fig. 146). Within Epeolini, the restriction of the preoccipital carina to the gena, 21(4) (Fig. 33), and the down-turned distal plane of male pygidial plate, 58(1) (Fig. 22C), are characters unique to some (but not all) species of *Triepeolus*.

The New World species of *Triepeolus* form a monophyletic group, segregated from the Old World species based on the following characters: the presence of the preoccipital carina only on the gena, 21(4) (also on the dorsal edge of head in *Triepeolus distinctus* and *Triepeolus epeolurus*); the relatively short female F1 relative to F2, 11(0); the absence of the basitibial plate, 47(0) (partially present in *T. epeolurus*); the elongate lateral process of the female T7, 59(1) (not elongate in *T. epeolurus*); the absence of elongate or curved setae on the apex of the male S3, 63(0); and the emarginate ventral margin of the male gonocoxite, 94(1).

Comments.—Although the number of maxillary palpal segments is widely recognized to be unstable and therefore of relatively little use in phylogenetic reconstruction, *Triepeolus* species (except for *Triepeolus nobilis*) tend to have either three or two maxillary palpal segments (if only two segments, then the distal segment is elongate). This is unlike most other Thalestriina, which tend to have two, relatively small and ovate maxillary palpal segments.

A diverse array of morphological variation is present among species of *Triepeolus*, especially in characters of the tibiae, the pseudopygidial area, the pygidial plate of both males and females, and the female S5 and S6. The diversity of pseudopygidial forms within *Triepeolus* is particularly pronounced (Figs. 186–189). In *Triepeolus*, most pseudopygidial setae reflect a golden color, although silvery reflective setae are present in *Triepeolus epeolurus*.

KEY TO THE GENERA OF EPEOLINI

1. Body largely covered by bright metallic blue or green scale-like setae .... *Thalestria*

— Body lacking bright metallic blue or green scale-like setae 2

2(1). Inner margins of compound eyes roughly parallel (Fig. 166); metasoma lacking apical bands of appressed setae; pterostigma relatively long (5 times longer than prestigma; Fig. 51); mesotibia lacking spine-like setae on posterior surface .... *Odyneropsis*

— Inner margins of compound eyes converging below (Figs. 167–169); metasoma rarely lacking apical bands of appressed setae; pterostigma relatively short (about 3 times longer than prestigma; Fig. 53); mesotibia with spine-like setae on posterior surface (Fig.172) 3

3(2). Scutellum with median longitudinal strip of appressed setae present between convexities; pseudopygidial area with apical margin strongly concave, bearing medioapical slit that is fringed on posterior margin with relatively long, curved, simple setae (Fig. 179); F1 relatively long (greater than length of F2) .... *Rhogepeolus*

— Scutellum rarely with distinct median longitudinal strip of appressed setae; pseudopygidial area variable but rarely strongly concave and not bearing medioapical slit; length of F1 variable, but not greater than length of F2 4

4(3). Males 5

— Females 9

5(4). Scape dramatically swollen or forming sub-basal angle on plical surface; metafemur with elongate setae on undersurface (rarely lacking); preoccipital carina complete or absent at upper corners of head (Figs. 31 and 32); basitibial plate completely bordered by carina; S3 with elongate, curled setae on apical margin .... *Doeringiella*

— Scape variable but not swollen, not forming sub-basal angle on plical surface; metafemur very rarely with elongate setae on undersurface; preoccipital carina variable; basitibial plate absent to completely bordered by carina; S3 with apical setae variable, rarely curled 6

6(5). Supraclypeal area produced into bulbous protrusion with weak median carina (Fig. 168); preoccipital carina continuous on head (Fig. 30); scutum with median longitudinal band of appressed setae (sometimes faint); scutellum relatively flat, bearing two mammiform tubercles; second abscissa of hindwing vein M+Cu over twice as long as cu-a ....*Rhinepeolus*

— Supraclypeal area and median carina variable, rarely produced into bulbous protrusion; preoccipital carina absent at least on upper corners of head (Figs. 32 and 33); scutum usually lacking median longitudinal band of appressed setae (sublateral bands can be present); scutellum variable but not bearing mammiform tubercles; second abscissa of hindwing vein M+Cu usually less than twice as long as cu-a......... 7

7(6). Scape relatively short (length approx. 1.5 times width), flattened on condylar surface; labrum with median process on apical margin between lateral tubercles (Fig. 37); basitibial plate incompletely or rarely completely bordered by carinae; preoccipital carina absent on upper corners of head (Fig. 32); S3 with straight, elongate setae on apical margin .... *Pseudepeolus*

— Scape length variable, not flattened on condylar surface; apical margin of labrum variable; basitibial plate absent or rarely incompletely bordered by carinae; preoccipital carina absent on at least upper corners of head; S3 with setae usually undifferentiated on apical margin, rarely elongate or curled 8

8(7). Mandible lacking distinct preapical tooth; pygidial plate usually with median constriction, often apically differentiated into distinct, down-turned, posterior surface (Fig. 22C), or present as an elongate, narrow structure; S7 usually with median emargination on distal margin, with lateral lobes below interlobal area, and apical setae mostly ventral, forming distinct pocket near lateral apical lobe (Figs. 85–95); gonostylus lacking basal lobe (Fig. 128B); penis usually lacking lateral projections (Fig. 146) or sometimes with subapical, lamellate projection; dorsobasal lobe of penis valve covering basolateral margin of penis; antennal pedicel usually set into scape...... *Triepeolus*

— Mandible usually with preapical tooth (Fig. 39); pygidial plate almost always all in one plane, broadly rounded posteriorly; S7 usually lacking median emargination on distal margin, with lateral lobes above interlobal area, and with apical setae mostly dorsal, on surface leading from lateral lobe (Figs. 68–76); gonostylus with basal angle or lobe (Fig. 129); penis with widely divergent, fleshy lateral lobe (Fig. 141), or lacking in *Trophocleptria*, sensu Michener, 2000 (Fig. 142); dorsobasal lobe of penis valve not enlarge, not covering basolateral margin of penis; antennal pedicel usually mostly exposed.. *Epeolus*

9(4). Lateral processes of S6 spatulate, with apical principal setae forming small denticles (Fig. 13); pseudopygidial area forming wide lunule of silvery setae on apical margin; apical ventral surface of pygidial plate with two medial, flattened, rounded processes, sometimes very reduced (Fig. 176) ....*Epeolus*

— Lateral processes of S6 rod-like, with apical principal setae elongate and hooked (Figs. 7 and 22B); pseudopygidial area variable, very rarely forming wide lunule of silvery setae on apical margin (silvery setae present rarely); apical ventral surface of pygidial plate with lateral, scroll-like processes (Fig. 178) 10

10(9). Supraclypeal area produced into bulbous protrusion with weak median carina (Fig. 168); scutellum relatively flat, bearing two mammiform tubercles; pseudopygidial area with median longitudinal row of dark, stout setae, and with apical margin convex (Fig. 183); preoccipital carina continuous on head (Fig. 30); second abscissa of the hindwing vein M+Cu over twice as long as cu-a ....*Rhinepeolus*

— Supraclypeal area not bulbous, with strong or weak protrusion and carina; scutellum variable but not bearing mammiform tubercles; pseudopygidial area variable but lacking median, longitudinal row of dark, stout setae; preoccipital carina forming angles at upper corners of head or absent on at least dorsal corners of head (Figs. 31–33); second abscissa of hindwing vein M+Cu variable..............................11

11(10). Scape length about twice its width, forming sub-basal angle on plical surface; preoccipital carina complete or absent at upper corners of head (Figs. 31 and 32); basitibial plate completely bordered by carina; F1 and F2 of about same length .... *Doeringiella*

— Scape usually only 1.5 times its width, rarely twice, not forming sub-basal angle on plical surface; preoccipital carina absent at upper corners of head or along entire upper border of head (Figs. 32 and 33); basitibial plate absent to completely bordered by carina; F1 usually shorter than F2, rarely the same length 12

12(11). Scutum almost always with elongate longitudinal bands of appressed setae reaching middle; basitibial plate absent or incomplete; preoccipital carina absent on upper corners of head or along entire upper border of head (Figs. 32 and 33); labrum with apical margin variable; maxillary papus with two or three segments (Figs. 26–28)...............................*Triepeolus*

— Scutum with longitudinal bands of appressed setae often reduced, usually restricted to anterior fourth; basitibial plate incompletely or rarely completely bordered by carina; preoccipital carina absent at upper corners of head only (Fig. 32); labrum with apical margin bearing median process (Fig. 37); maxillary palpus usually with two small segments (Fig. 28) ....*Pseudepeolus*

DISCUSSION

The monophyly of Epeolini and its subtribes, and the phylogenetic relationships of these subtribes to one another, are strongly supported by several synapomorphic characters (Fig. 19a, and comments under the systematics treatments of Epeolini, Odyneropsina, Rhogepeolina, Epeolina, and Thalestriina, above). The monophyly of Epeolini was also supported by shared features of the labrum and spiracles of mature larvae in an analysis prepared by Rozen (1996). *Odyneropsis* is resolved as the basalmost lineage of the tribe, rather than sister to *Rhogepeolus*, as was suggested by some previous workers (see Comments under *Odyneropsis*). *Rhogepeolus* is instead resolved as sister to the rest of Epeolini due to several synapomorphic features of the mandibular articulations, compound eyes, hindwing veins, setae of the metatibia, and male S4 and S7. *Epeolus* and Thalestriina form a clade based on shared features of the male S7, dorsal connecting bridge of the penis valves, and setae on the forewing and male S5.

The phylogeny of the genera within Thalestriina is poorly resolved (Fig. 19b), and the restricted phylogenetic analyses of Thalestriina (Fig. 20) produced different topologies than was produced by the analysis of the entire tribe. The only resolved clades within Thalestriina that were moderately robust to outgroup selection were the clades (*Rhinepeolus* + *Pseudepeolus*) and (*Doeringiella* + *Thalestria*). *Rhinepeolus* and *Pseudepeolus* share the trait of not having the inner and outer margins of the female S6 strongly converging near the mediolateral apodeme, as is found in the other genera of Thalestriina (particularly *Triepeolus* and *Doeringiella*). *Doeringiella* and *Thalestria* share the prominent depression on the frons behind the scape and the long setae on the underside of the male mesofemur (although such setae are also present in basal *Pseudepeolus*, according to Compagnucci and Roig-Alsina, 2003). None of the clades resolved by these analyses have been previously proposed and I do not consider them to be sufficiently supported to merit their recognition in a new classification scheme. Additional study of this subtribe is needed; it would be desirable to add characters from other sources, such as the eggs, larvae, and DNA sequence data. Rozen (1996) found mature larval characters of the mandibles and maxillary palpi that vary within Thalestriina and Epeolini as a whole;

unfortunately, the immatures of *Rhinepeolus* and *Pseudepeolus* are still not known, and a more detailed examination of *Doeringiella* larvae is desirable before such an analysis can be undertaken.

The present study was not designed to address which outgroup tribe is sister to Epeolini, and any resolution in topology at this level should be considered tentative. However, *Brachynomada* is resolved as the nearest outgroup to Epeolini based on the presence of a paraocular carina and a distinct distal process on the male S7. A sister-group relationship of Brachynomadini with Epeolini seems intuitively pleasing given the similarity of both the male S7 and S8 (Figs. 55, 60, 64–127). However, the paraocular carina is weaker in *Brachynomada* than in epeolines, and *Brachynomada* differs strikingly from Epeolini (and other nomadines) by the lack of principal setae on the female S6 (Fig. 5).

Hexepeolus is resolved as sister to *Nomada*, supported by a number of homoplastic characters. Roig-Alsina and Michener (1993) code *Hexepeolus* and some members of *Nomada* as lacking a flabellum, a character which might provide additional support for this relationship. Alternatively, *Hexepeolus* shares with Epeolini a few seemingly strong synapomorphies. They include the sclerotized galea, and according to Alexander (1990), the postgenal bridge of the lower occipital area interrupted by a median longitudinal trough.

Although this study was similarly not designed to resolve the internal relationships of genera, some interesting patterns are worth mentioning. Old World taxa are resolved as basal within *Epeolus*, with the African species, *Epeolus natalensis*, segregated as a lineage basal to the European and New World taxa. This result parallels Alexander's (1994) hypothesis that South African *Nomada* are basal within Nomadini. Additionally, in some most parsimonious trees (not shown), *Epeolus lectoides* is grouped with *Epeolus bifasciatus* and *Epeolus variolosus* based on the apically emarginate sides of the medioapical process of the male S8; also, *E. lectoides* has a shining area in the same position that the other two species bear a waxy protrusion (although the latter condition is shared by several other North American *Epeolus*; Brumley, 1965, and personal observation). However, unlike all other examined *Epeolus* species, *E. lectoides* bears a distinct, sub-basal digitiform appendage on the basal apodeme of the female S6 (Fig. 8). This feature resembles the Thalestriina-type S6 basal apodemal appendage, and therefore might suggest a less derived position of this species within *Epeolus*.

Old World species of *Triepeolus* were similarly recovered as basal in the present phylogenetic analyses, with *Triepeolus tristis* basal to *Triepeolus ventralis*. An additional clade of *Triepeolus* was unambiguously resolved composed of *Triepeolus ancoratus*, *T. lunatus*, *T. quadrifasciatus*, and *T. vicinus*. This clade is supported by the presence of three maxillary palpal segments, 2(3); the basally tubular and apically spatulate setae of the pseudopygidial area, 55(1) (Fig. 188B); the circular, down-turned distal plane of the male pygidial plate, 58(1) (Fig. 22C); the apical, ventrally directed lip of the female S5, 67(1); the straight, bar shaped disk that is roughly perpendicular to the inner margins of the apical processes of the female S6, 69(3) (Fig. 9); and the rounded lateral margins of the distal process of the male S7, 86(3) (Figs. 88, 90, 91, and 94). Many of these characters are homoplastic and it remains to be seen if the clade will be recovered in a more robust analysis of the genus. The internal relationships of *Triepeolus* will be examined in a forthcoming phylogenetic study (Rightmyer, in prep.).

Based on the results of this study, the tribe Epeolini likely originated and initially diversified in the Neotropics, with some of the lineages subsequently dispersing to other regions. If the tentative internal phylogenies of *Epeolus* and *Triepeolus* are correct, the basal species of both genera are found in the Old World. One explanation for this pattern might be that these epeolines were able to reach Africa when it was still in close proximity to South America. An early African lineage of *Epeolus* may have then successfully diversified in the Old World, while lineages of both *Epeolus* and *Triepeolus* concurrently experienced large radiations in North America. However, this scenario would rely on the extinction of New World *Triepeolus* and *Epeolus* stem lineages, and on the retention of plesiomorphic traits in Old World species. It would also rely on the extinction of *Triepeolus* in Africa and the Middle East, with the few known Palearctic *Triepeolus* representing the lone survivors of this African radiation. An alternative hypothesis is that stem lineages of *Epeolus* and *Triepeolus* might have obtained a Holarctic distribution by dispersing over Beringia, with subsequent Paleartic/Nearctic vicariance, and further dispersal of *Epeolus* into Africa from the Palearctic (a similar scenario was proposed by Ascher, 2004, for Andrenidae). Unfortunately, the fossil record of Nomadinae is unknown and so cannot help shed light on the origin and diversification of epeoline bees; however, the fossil record of other insect taxa shows that several groups now endemic to the southern hemisphere once had northern distributions (Engel, 2001). Discussion of the likelihood of such scenarios is postponed until more robust phylogenies of these genera are produced.

Despite the relatively great diversity of genera in the Neotropics, the two genera with the greatest number of species and the widest distributions are not especially diverse in that region. Of the approximately 150 species of *Triepeolus*, only 10 are known from the Neotropics; similarly, *Epeolus* appears to have the largest number of species in North and Central America and the Palearctic (Michener, 2000). If host diversity helps to drive parasite cladogenesis, then the relative lack of eucerine diversity in the Old World may help explain the paucity of *Triepeolus* species there. In contrast, the relative numbers of species of *Triepeolus* in North America as opposed to South America is enigmatic; eucerines are relatively abundant throughout the New World and have a higher generic diversity in South America (Michener, 2000). Similarly, the high diversity of *Colletes* in South America does not correlate well with relative scarcity of *Epeolus* there, although it may be correlated with the evolution of species of *Epeolus* with remarkable synapomorphies, such as the primarily Neotropical group *Trophocleptria*. The high species diversity of these parasite genera in the Nearctic may simply reflect the general trend for higher parasite diversity in temperate, particularly xeric, regions because of the role that high seasonality plays in synchronizing host and parasite ontogeny (Wcislo and Cane, 1996). It may also simply be that *Triepeolus* and *Epeolus* diversified primarily in the Holarctic, and that species in the Neotropics represent lineages that dispersed southwards from North America.

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APPENDIX 1

Triepeolus epeolurus New Species

Because of its unusual features, an undescribed species was included in the phylogenetic analysis. The species is described here in order to make its name available.

Triepeolus **epeolurus** new species
(Figs. 21–22, 36, 93, 123, 128, 151, 164, 189)

Diagnosis.—Females of this species are readily distinguished from females of other *Triepeolus* by the pseudopygidial area, which has a transverse, slightly curved band of silvery setae (Fig. 22A). The labrum of both males and females bears an apical scoop-like process resulting from the fusion of the two subapical tubercles (Fig. 36). The pedicel is not as recessed into the scape as it is in most other *Triepeolus*; additionally, unlike most species of this genus from the New World, the preoccipital carina is present on the dorsal margin of the head (Fig. 32), the basitibial plate is partially bordered by a carina, and the lateral process of the female T7 is not elongate (Fig. 164).

Description.—Female holotype: Total body length about 8.6 mm (8.6–10.6 mm range); forewing length 5.7 mm (5.7–6.8 mm range). Head width 3.0mm (3.0–3.3 mm range), length, excluding labrum, 2.0 mm (2.0–2.1 mm range) (Fig. 21). Maxilla with two maxillary palpal segments. Mandible simple. Labrum with two apically elevated tubercles fused into scoop like structure (Fig. 36; on some specimens these tubercles more distinct, but margin between tubercles remaining elevated); labrum about 1.5 times wider than long. Frontal carina strong on swollen supraclypeal area, becoming less pronounced on upper frons near median ocellus. Subantennal sulcus weakly arcuate inward, connecting to middle of antennal socket; subantennal sulcus about one-fourth longer than diameter of antennal socket. Antennal pedicel set into scape; pedicel about 1.5 times broader than long. Scape, excluding basal bulb, slightly more than two times as long as wide. F1 distinctly shorter than F2; F2–F9 subequal at longest points, F10 longest. Paraocular carina pronounced, ending dorsally at mid-frons. Interocellar distance 1.5 OD. Ocellocular distance just over 1.5 OD; distance from lateral ocellus to preoccipital ridge about 0.75 OD. Preoccipital carina strong along gena and upper border of head, broken at upper corner of head, which is not carinate. Width of gena about 0.5 width of compound eye at widest points. Compound eyes convergent below. Anterior margin of dorsal surface of pronotum slightly less convex than anterior margin of scutum (Fig. 21B). Intertegular distance 1.8 mm (1.8–2.0 mm range). Axilla triangular, not reaching apex of scutellum, spine with nar-

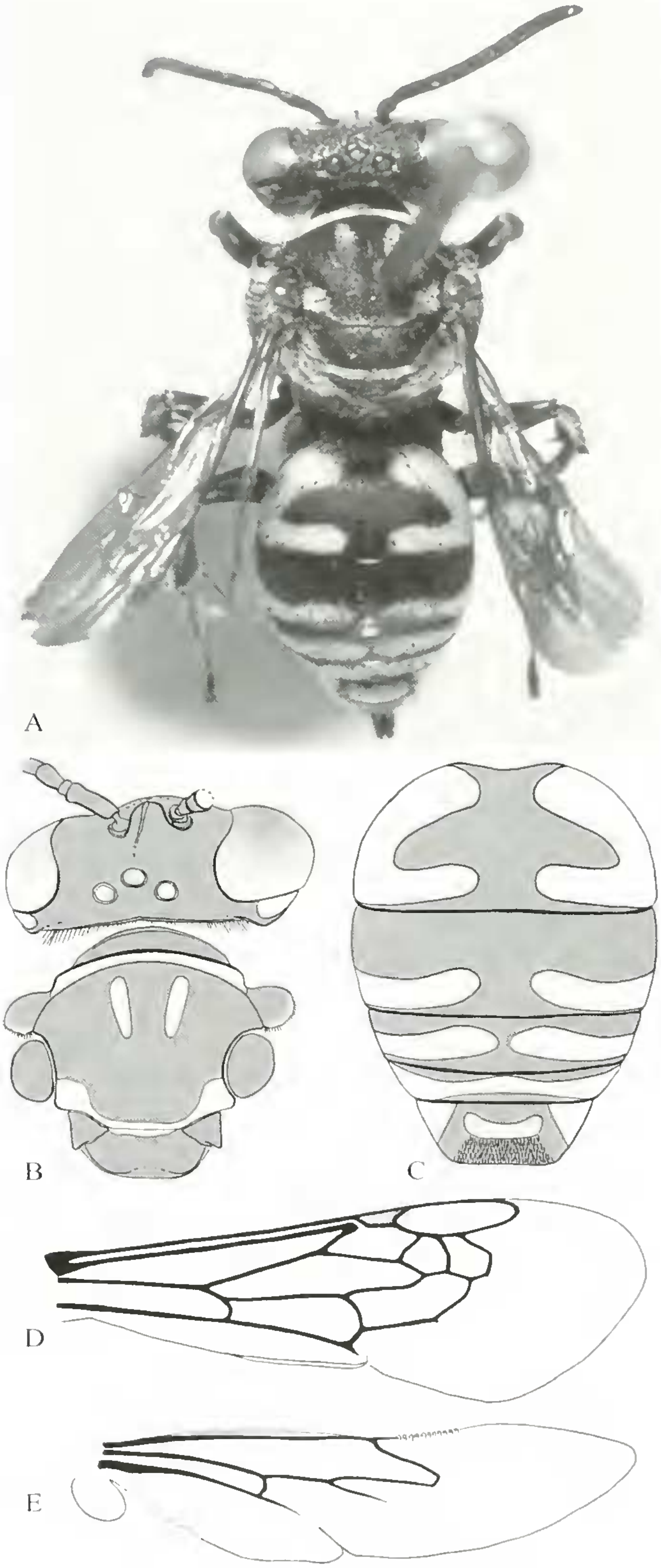


Fig. 21. *Triepeolus epeolurus*, new species. A. Dorsal habitus. B. Head and mesosoma. C. Metasoma. D. Forewing. E. Hindwing.

rowly rounded apical point. Scutellum modestly biconvex, lacking tubercles. Propodeal spiracle bordered dorsally by shelf-like carina and posteriorly by strongly angled integument. Mesotibial spur 0.6 times length of mesobasitarsus. Posterolateral angle of protibia produced into triangular spine. Posterolateral angle of mesotibia forming enlarged, triangular, carinate spine. Outer metatibial spur about 0.8 times length of inner metatibial spur. Basitibial plate indicated by slight concavity, lacking any clear border. Wings as in Figs. 21D and E. Carina at dorsolateral angle of T1 ending about 0.4 OD from apical margin. Metasomal terga lacking distinct, concave, marginal zone. Pygidial plate with longitudinal medial ridge. Seventh and eighth hemitergites as in Figs. 164 and 151; lateral process of T7 not elongate. S6 as in Fig. 22B; inner margin of process of S6 convex basally; basal apodeme of S6 with inner process reduced and not digitiform.

Body entirely black except apical three-fourths of mandible semitransparent, dark brownish red; antenna brownish black except area on anterior surface of F1, pedicel and scape basally near bulb orange-brown; legs (metatibia darkest), metasomal sterna, and lateral portion of T1 and T2 dark reddish brown; tegula brown with transparent, pale yellow margin. Wings pale brown, transparent. Ocelli pale orange-brown; compound eyes pale brown.

Mandible smooth apically, basally minutely imbricate with scattered small punctures. Labrum with punctures nearly contiguous (larger punctures about 0.08 OD in diameter), punctures becoming slightly larger and more widely spaced basally and laterally. Clypeus with irregularly spaced, small punctures (about 0.1 OD), punctures larger and more widely spaced apicolaterally. Supraclypeal area, integument below antennal sockets and vertex with nearly contiguous, minute punctures (about 0.05 OD). Upper frons with punctures more dispersed and enlarged (up to 0.2 OD), some separated by as much as one puncture width. Gena with regularly spaced, small punctures (0.1 OD). Pronotum, including pronotal lobe, with regularly spaced, small to minute punctures (0.05–0.08 OD). Scutum, scutellum and axilla with most punctures nearly contiguous (0.08–0.10 OD), punctures on scutum becoming less dense and coarser towards posterior half. Metanotum covered with appressed setation such that punctation is obscured. Metapostnotum lineolate; lateral and posterior surfaces of propodeum outside of triangle with regularly spaced punctures (about 0.08 OD), separated by slightly less than half a puncture diameter. Tegula with shallow, extremely minute punctures (0.02 OD) separated by two puncture widths; tegular margin impunctate. Mesepisternum dorsally, and hypoepimeron with small (0.10–0.15 OD), almost contiguous punctures; mesepisternum ventrally with punctures becoming larger and less densely spaced; mesepisternum and especially hypoepimeron posteriorly near pleural sulcus nearly impunctate. Metepisternum with punctures nearly contiguous and minute (about 0.05 OD). Outer surfaces of legs with shallow, min-

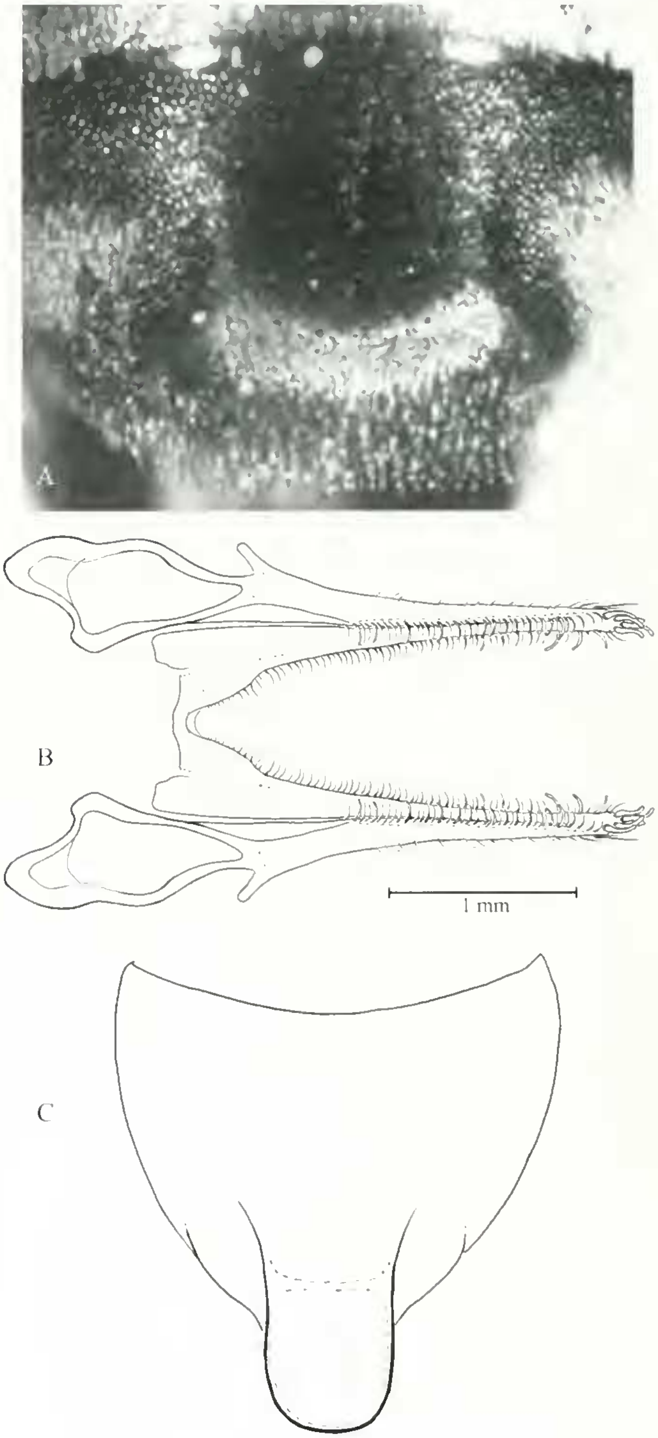


Fig. 22. *Triepeolus epeolurus*, new species. A. Female T5, showing silvery band of setae on pseudopygidial area. B. Female S6, ventral view. C. Male T7.

ute punctures, nearly contiguous to separated by two puncture widths, these punctures becoming exceedingly faint on outer surfaces of femora and tibiae; inner surfaces of femora and tibiae with impunctate, finely imbricate areas. External metasomal terga and sterna with minute punctation (0.05 OD); punctures contiguous to separated by a puncture diameter on terga, nearly contiguous to separated by two puncture diameters on sterna. T1–T5 with narrow (about 0.15 OD), impunctate, apical margins.

Mandible with sparse, golden, simple setae (about 0.2–1.5 OD in length) in acetabular, outer and condylar grooves, and white, minute, branched setae (about 0.2 OD) near base of mandible. Labrum with white, branched, subappressed setae (about 0.3 OD) in medial concavity formed by ridges connecting to apical tubercles, and in scoop-like structure formed by apical tubercles; elsewhere on labrum, golden, simple setae (about 0.4 OD) sparsely interspersed with pale, branched setae (about 0.2 OD), the simple setae longer and denser at apical half of labrum. Face between compound eyes at level of supraclypeal area, excluding immediate vicinity of frontal carina, covered with appressed, white, plumose setae (about 0.75–1.0 OD); clypeus with these white setae much less dense (about 0.25 OD), intermixed with scattered, nonappressed, simple setae (0.5–1.0 OD). Medial-facing surface of scape with appressed, minutely branched, white setae (about 0.25 OD). Frons lacking setae immediately behind antennal sockets, otherwise with scattered, pale golden, suberect, simple setae (about 0.8–1.0 OD), setae becoming denser immediately posterior to median ocellus; vertex with sparse, minute, white, branched and simple setae (about 0.05 OD); upper preoccipital carina and upper corners of head with band of white, minutely branched setae (0.25 OD); occipital area with pale, erect, simple setae (0.2 OD medially to 1.0 OD laterally). Gena densely covered with white, appressed, branched setae (0.2 OD) in triangular pattern along margin of compound eye, widest dorsally; gena otherwise lacking setae or sparsely covered with minute, branched setae. Anterodorsal surface of pronotum with minutely branched, dusky setae (0.2 OD); lateral surface of pronotum largely lacking setae; dorsal collar of pronotum and margins of pronotal lobe with dense, pale yellow, plumose setae (about 0.5 OD). Scutum, especially near margins (but not intermixed with pale yellow, branched setae, see below), posterior surface of scutellum, and axilla (especially on undersurface of spine) sparsely covered with dark brown, subappressed, branched setae (about 0.3 OD); these segments, especially on disk of scutum and dorsal surface of scutellum, also sparsely covered with dark brown, simple, suberect setae (about 0.3 OD). Pale yellow, appressed, plumose setae forming two lines lateral to midline of scutum, starting about 1.5 OD from anterior margin and ending just before midpoint of scutum; pale yellow, appressed setae also along lateral margin of scutum posterior to axilla, at posterior margin near scutellum, and on anterior margin of scutellum near scutum. Metanotum densely covered with pale yellow, short, appressed, medially directed, plumose setae (about 0.25 OD). Cream colored, finely branched setae emerging from lateral metanotal area immediately behind wing base (about 2 OD). Posterior surface of propodeum, excluding triangle, with appressed, laterally directed, branched setae, these setae white on upper third of propodeum (ending at upper, shelf-like carina of propodeal spiracle, about 0.2 OD), dark and less dense on lower two-thirds of propodeum (about 0.1 OD). Mesepisternum near pronotal lobe with sparse area of white, branched setae (about 0.2 OD). Posterior half of mesepisternum below hypoepimeron to above dorsal level of mesocoxal-pleural articulation densely covered with white, branched setae (about 0.4 OD); mesepisternum just below dense patch of white setae, metepisternum and lateral surface of propodeum below spiracular carina with dark brown, branched setae (about 0.1 OD). Hypoepimeron with scattered white, branched setae, ventrally intermixed with few dark brown, branched setae. Propodeum with dense area of white, branched setae along spiracular carina. Venter of mesosoma covered with posteriorly directed, branched setae, these setae dark anteriorly, becoming pale near mesocoxae. Setae of outer surfaces of coxae branched, with basal setae dark, apical setae white. Outer surfaces of femora medially almost glabrous, laterally and apically with branched fuscous setae grading into pale setae. Outer surfaces of tibiae more densely covered with white, branched setae, sparsely interspersed with few simple, fuscous setae; apical margin of protibia with few spine-like setae; outer surface of mesotibia bordered anteriorly with brush of golden, simple setae; posterior facing surface of mesotibia, and outer and posterior facing surfaces of metatibia with scattered stout, simple setae arising from partially flattened tubercles; apical posterolateral corner of metatibia covered with dense patch of dark, simple setae. Inner surfaces of femora, protibia, and mesotibia almost lacking setae; metatibia and basitarsi with inner surfaces covered with dense, brush like mat of simple golden setae, those of metatibia 0.2–0.3 OD in length, those of basitarsi (especially metabasitarsus) elongate (about 0.4–0.5 OD). Wings covered with short simple setae (about 0.1 OD) with nearly bare areas basally near veins. Except as noted elsewhere, metasomal terga covered with minute, branched, dark, setae (about 0.1 OD); in dorsal view, T1 basally and T1–T4 apically and laterally with areas of dense, appressed, white, branched setae (about 0.1–0.2 OD; Fig. 21C). T1–T4 with apical margin glabrous. Pseudopygidial area of T5 basally with dense, shining, transverse, silvery band of appressed, flattened, simple setae, grading apically to stout, more sparsely spaced, golden, simple, hooked setae (Figs. 21C, 22A, and 189A). Basal to pseudopygidial area, T5 with dark, finely branched, hooked setae (Fig. 189B; these setae appear stout and simple under dissecting microscope); lateral to that, T5 with dense, triangular patch of white, appressed, branched setae. T6 with simple, apically hooked setae on pygidial plate (0.2–0.4 OD) and longer, finely branched setae lateral to plate (longest about 1.25 OD). S2–S4 medioapically with dark, subappressed, branched setae, elsewhere with white, subappressed, branched setae, these white setae becoming longer distally (0.05–0.2 OD). S5 entirely covered with dark, subappressed, branched setae (about 0.2 OD).

Male: Agrees with female, except for usual sexual features and the following: setation slightly denser on labrum and clypeus. F1 distinctly shorter than F2 only on outer lateral margin. Orange-brown coloration on antenna limited to basal portion of scape near basal bulb, if present at all (otherwise entirely dark brown). Setae slightly longer and denser on meso- and metatibiae, obscuring stout, simple setae arising from tubercles. Metatibia lacking dense patch of dark simple setae on posterolateral angle. Tarsi dark reddish brown; legs otherwise dark brownish black. T7 densely covered with long, brown, branched setae except on and beneath pygidial plate; setae on pygidial plate sparse, simple, and dark; those beneath plate elongate, simple to minutely branched. Pygidial plate as in Figure 22C; plate bordered entirely by carina (in some specimens this carina less distinct along apical margin, possibly due to wear), distinctly angulate in profile (forming dorsal and posterior surfaces); posterior surface almost impunctate (basally with few, shallow punctures). S2–S3 with white, branched setae sparsely covering entire surface (about 0.07–0.5 OD); those on apex of S3 0.3 OD, but those on apex of S2 0.5 OD; apical margin of S3–S4 with elongate fringe of finely branched, dusky setae curved medially and posteriorly (about 1.0–1.5 OD). S6 densely covered with dark, branched setae (0.5 OD). S7 with apical field of setae on ventral surface; S7 and S8 otherwise as in Figures 93 and 123. Genital capsule as in Figure 128. T7 with punctures (0.1–0.2 OD) on dorsal facing surface of pygidial plate and lateral to pygidial plate almost contiguous to separated by one puncture width; basal disk of T7 similar to other visible terga. Disk of T7 and dorsal facing portion of pygidial plate with branched, subappressed, dark setae (about 0.1 OD basally to 0.5 OD apically); posterior facing portion of pygidial plate with scant, short, erect, simple, dark setae (about 0.25 OD); lateral to, and below, pygidial plate with long, simple to minutely branched, dark setae (about 0.6 OD).

Material examined.—Holotype female: **MEXICO, Michoacán**, Los Sabinos, 28 km S Ario de Rosales, 1190m, 29-X-1987, LG-249 / / L. Godinez Collector (SEMC). Paratypes: (all from **MEXICO**), **Michoacán**, Los Sabinos: 1 ♂, 24 km N La Huacana, 1190m, 29-X-1987 / / R. Ayala Collector (EBCC); 2 ♀♀, 1 ♂, 24 km N La Huacana, 1190m, 30-X-1987 / / R. Ayala Collector (EBCC); 1 ♀, 28 km S Ario de Rosales, 1190m, 29-X-1987, LG-249 / / L. Godinez Collector (SEMC); 1 ♂, 28 km S Ario de Rosales, 1190m, 29-X-1987, LG-245 / / L. Godinez Collector (SEMC); 2 ♀♀, 28 km S Ario de Rosales, 1190m, 29-X-1987, LG-252 / / L. Godinez Collector (SEMC). **Jalisco**: 1 ♂, Chamela, Río San Nicolas, 5-X-1985, Col. R. Ayala / / *Triepeolus* sp. 3 (EBCC); 1 ♀, 1 ♂, Chamela, 1/8-X-85, F.D. Parker, T.L. Griswold / / *Triepeolus* sp. 25, Griswold det. (BLCU); 1 ♀, 14km. N. Guadalajara, Ruta 54, Posada San Isidro, 22-IX-1986, R. Miller and L. Stange (FSCA); 12 ♀♀, 4 ♂♂, Estación Biología Chamela, 15-X-99, Chemsak (EMEC). **Oaxaca**: 1 ♀, 3mi. S. El Camerón, 2-X-1986, R. Miller and L. Stange (FSCA). Additional material: 1 ♀, **COSTA RICA**: **Guanacaste**, Finca Montezuma, 3 km SE Rio Naranjo, 28 XI–5XII 1991, F. Parker (BLCU). I find no features that differentiate this specimen from the type material; however, I have not dissected the genitalia to make further comparisons.

Etymology.—The specific epithet *epeolurus* is Greek: *epeol-* referring to the genus *Epeolus*, *-urus* meaning tail. The name is used in reference to the distinctive silvery band in the pseudopygidial area of the females, which resembles that found in species of *Epeolus*.

APPENDIX 2.

Characters used in the cladistic analyses.

Character-state zero is not necessarily plesiomorphic.

Head.

1. *Galea*: (0) weakly sclerotized, flexible, with apex pointed or narrowly rounded; (1) strongly sclerotized, stiff, with apex broadly rounded.
2. *Maxillary palpal segment number*: (0) 1 (Fig. 29); (1) 2, the distal segment small and ovate (Fig. 28); (2) 2; the distal segment elongate (Fig. 27); (3) 3 segments (Fig. 26); (4) 5 segments (Fig. 25); (5) 6 segments (Figs. 23 and 24).

   I have coded two palpal segments (distal segment elongate) as a character-state separate from two palpal segments (distal segment small and ovate) because I have found no gradations between the two. Some individuals (e.g., *Rhogepeolus bigibbosus*) were polymorphic with two palpal segments (the distal segment elongate) in one palpus and three palpal segments in the other, leading me to suspect that the elongate segment may result from the fusion of two smaller segments. No specimens were polymorphic for two segments with the distal segment small on one palpus and elongate in the other.
3. *Mandibular articulations*: (0) both in contact with compound eye; (1) only posterior articulation in contact with eye.
4. *Labrum with two submedial apical or subapical tubercles* (Figs. 34, 35, and 37): (0) absent; (1) present.
5. *Labrum with apical margin*: (0) straight or approximately continuous with slope of lateral labral margin (Fig. 35); (1) concave between

apical tubercles (Fig. 34); (2) forming a process, this process sometimes minute (Fig. 37); (3) elevated, continuous with elongate apical tubercles (Fig. 36).

6. *Mandible with distinct preapical tooth*: (0) absent (Fig. 40); (1) formed of trimmal extension, such that tooth is relatively medial on mandible and directed towards inner surface (Fig. 39).

The preapical tooth found in *Biastes brevicornis* was not considered homologous to those found in some Epeolini (i.e., character-state 1) because it is formed at the terminus of the acetabular carina, such that the tooth is relatively apical on the mandible and directed apically, as opposed to being an extension of the trimma. Thus, *B. brevicornis* was coded as having character-state 0.

7. *Frontal line*: (0) weakly carinate (Fig. 168); (1) strongly carinate (Fig. 167).

8. *Supraclypeal area*: (0) flat, not noticeably produced above plane of face; (1) produced, receding evenly from frontal carina to subantennal sutures (Fig. 166); (2) produced into roughly pentagonal-shaped swelling; (3) forming bulbous protrusion between antennal sockets (Fig. 168); (4) forming bulbous protrusion with lateral processes (Fig. 169).

9. *Clypeus with faint carina extending from end of frontal line*: (0) absent; (1) present.

10. *Lateroclypeal carina of males*: (0) absent; (1) present, well-separated from compound eyes (Fig. 40); (2) present, forming almost continuous carina with paraocular carina (Fig. 39).

Roig-Alsina (1991) noted that the presence of the lateroclypeal carina is variable within male *Nomada*; in *Nomada pampicola* the carina is absent.

11. *Longest length of female F1/F2*: (0) less than or equal to 0.75; (1) about 1; (2) greater than or equal to 1.25.

12. *Antennal pedicel of males*: (0) set into apex of scape, exposed part of pedicel thus 1.5 or more times as broad as long; (1) more fully exposed, only slightly broader than long or as broad as long.

13. *Scape length/width, excluding basal bulb*: (0) less than 1.5; (1) 1.5–1.7; (2) 1.8–2.0; (3) greater than 2.0.

Only females were coded for species of *Doeringiella* whose males have swollen scapes.

14. *Female scape with sub-basal angle on plical surface*: (0) absent; (1) present.

As defined in Roig-Alsina (1989), the plical surface is the surface of the scape toward which the flagellum is flexed.

15. *Frons with prominent depression behind scape*: (0) absent; (1) present (Fig. 167).

I have coded *Rhogepeolus emarginatus* as lacking this character; the deep pit found on the frons of this species is not homologous to the more evenly concave areas present in *Doeringiella* and *Thalestria*.

16. *Paraocular carina*: (0) absent (Fig. 40); (1) present (Fig. 39).

17. *Compound eyes of males*: (0) converging below (Fig. 167); (1) parallel (Fig. 166).

18. *Interocellar distance/width of lateral ocellus (approximate)*: (0) 1.0; (1) 1.5–2.0; (2) 2.5.

19. *Glabrous lobe between compound eye and lateral ocellus*: (0) absent; (1) present, shining and relatively flat; (2) present, enlarged and not shining, waxy in appearance (Fig. 42).

20. *Gena with swollen protrusion on dorsal area*: (0) absent; (1) present, not pronounced (Fig. 41); (2) present, pronounced (Fig. 42).

21. *Preoccipital carina*: (0) absent; (1) continuous, forming a smoothly rounded curve (Fig. 30); (2) continuous, forming angles at the upper corners of head (Fig. 31); (3) discontinuous, present only on gena and dorsal edge of head behind vertex (Fig. 32); (4) on gena only (Fig. 33).

Mesosoma.

22. *Pronotum with dorsal, anterior margin*: (0) straight or nearly so (Fig. 44); (1) convex (Fig. 45).

23. *Pronotum with dorsal, posterior surface, at midline of scutal margin in dorsal view*: (0) not visible, scutum overhanging pronotum at midline (Fig. 43); (1) visible, length much less than 1 OD (Fig. 44); (2) visible, length approximately equal to 1 OD (Fig. 45).

24. *Pronotum with dorsal, posterior surface, in lateral view*: (0) near plane of dorsal surface of scutum, continuous with curve of scutum (Fig. 50); (1) below plane of dorsal surface of scutum (Fig. 49); (2) greatly below plane of dorsal surface of scutum, anterior part of scutum arching above pronotum (Fig. 48).

25. *Scutum with longitudinal band of appressed setae on midline*: (0) absent; (1) present.

26. *Scutum with submedial longitudinal bands of appressed setae on anterior half*: (0) absent; (1) present as two short bands on anterior end of scutum, with bands sometimes reduced to dots; (2) present as two long bands extending to middle of scutum.

27. *Scutellum with two convexities*: (0) absent; (1) present, weak; (2) present, pronounced.

28. *Scutellum with carinate or flattened projections overhanging posterior surface of scutellum*: (0) absent; (1) present.

Character-state 1 is considerably more pronounced in *Epeolus variolosus* than in *Epeolus bifasciatus*.

29. *Scutellum with two mammiform tubercles*: (0) absent; (1) present, weak; (2) present, enlarged.

30. *Scutellum with color sexual dimorphism*: (0) absent; (1) present, with female scutellum red, male black.

31. *Scutellum with distinct median longitudinal strip of appressed setae*: (0) absent; (1) present.

32. *Axillar spines*: (0) absent; (1) present.

33. *Axillar spines with pronounced carinate ridge*: (0) absent; (1) present, defining dorsal edge (Fig. 46); (2) present, defining lateral edge (Fig. 47).

Several other species of *Epeolus* that were examined (e.g. *Epeolus cruciger*, *Epeolus lectoides*, and others) appear to have a similar but much weaker carina on the axilla.

34. *Forewing setae on radial cell*: (0) dense on entire or majority of cell; (1) restricted to costal half or less of cell (along Sc+R); (2) sparse, scattered.

35. *Pterostigma length/ prestigma length (about)*: (0) 1.5 (Fig. 52); (1) 3 (Fig. 53); (2) 5 (Fig. 51).

36. *Forewing vein r-rs*: (0) arising from point distal to midpoint of pterostigma (Figs. 52 and 53); (1) arising from midpoint of pterostigma (Fig. 51).

37. *Length of all submarginal cells together*: (0) distinctly greater than length of marginal cell (Figs. 52 and 53); (1) approximately equal to length of marginal cell (Fig. 51).

38. *Vein 2rs-m*: (0) extending to, or slightly distal to, midpoint of marginal cell (Figs. 52 and 53); (1) basal to midpoint of marginal cell (Fig. 51).

39. *Forewing with papilliform setae distal to cells*: (0) absent; (1) present.

40. *Hindwing with second abscissa of vein M+Cu*: (0) at least twice as long as cu-a, usually as long as or longer than M; (1) less than twice as long as cu-a, approximately one-half to three-fourths as long as M; (2) less than twice as long as cu-a, much less than half as long as M.

41. *Procoxa shape*: (0) roughly conical or pyriform, with trochanters close together; (1) roughly quadrate, with trochanters widely separated.

The procoxa is somewhat less quadrate in *Rhogepeolus* and some *Epeolus* than in other Epeolini.

42. *Male mesofemur with long setae on undersurface*: (0) absent; (1) present.

43. *Mesotibia with dense patch of golden, simple setae on anterior margin of outer surface*: (0) absent; (1) present (Fig. 172).

44. *Mesotibia with thick, spine-like setae on posterior-facing surface*: (0) absent; (1) few, scattered; (2) numerous.

45. *Female metatibia with apical, posterolateral surface*: (0) bearing setae similar to rest of lateral surface of metatibia; (1) less setose than rest of metatibia, but bearing spines (Fig. 173); (2) bearing dense patch of simple setae, with light reflecting from these setae differently (e.g., silvery or golden brown) than from surrounding setae (similar to that shown in Figs. 170 and 171).

46. *Metatibia with differentiated bases of spine-like setae*: (0) absent; (1) present, not enlarged; (2) present, dorsally enlarged (Fig. 174).

47. *Basitibial plate*: (0) absent or lacking distinct boundary; (1) not fully bordered by carina; (2) fully bordered by carina.

Metasoma.

48. *Metasoma with appressed setae*: (0) absent; (1) restricted to small spots on terga; (2) forming bands across terga

49. *Female [illegible] with branched setae*: (0) absent; (1) present at least lateral to pseudopygidial area
50. *Pseudopygidial area with apical margin*: (0) convex; (1) straight or nearly so; (2) concave
51. *Pseudopygidial area with medioapical slit*: (0) absent; (1) present (Figs. 179A and 181).
52. *Pseudopygidial area with silvery band*: (0) absent; (1) present, formed of rounded, flattened setae (Figs. 190 and 191); (2) present, formed of pointed, flattened setae (Figs. 22A, 189C).
53. *Pseudopygidial area with globular, deeply rugoso-striate setae*: (0) absent; (1) present (Fig. 180B).
54. *Pseudopygidial area with entirely tubular, apically blunt setae*: (0) absent; (1) present (Fig. 179B).
55. *Pseudopygidial area primarily with basally tubular, apically spatulate but pointed setae*: (0) absent; (1) present (Figs. 185B, 188B).
56. *Female pygidial plate with longitudinal median ridge*: (0) absent; (1) present.
57. *Female pygidial plate with apical ventral surface, in posterior view*: (0) with no obvious areas of thickening; (1) medially forming one rounded process, this process apparently derived from ventral surface of T5 (Fig. 175); (2) medially forming two flattened rounded processes, these processes apparently derived from ventral surface of T5 (Fig. 176; processes sometimes very reduced); (3) mediolaterally thickened into two triangular projections, these processes apparently derived from ventral surface of T5 (Fig. 177); (4) laterally forming enlarged triangular processes, these processes apparently derived from both ventral and lateral surfaces of T5; (5) laterally forming scroll-like processes, these processes apparently derived from lateral surface of T5 (Fig. 178).
58. *Male pygidial plate with distal surface*: (0) not distinctly differentiated from dorsal surface of plate; (1) facing posteriorly, distinct from dorsal surface of plate (Fig. 22C).
59. *Female T7 with lateral process (articulates with S6)*: (0) not elongate (Figs. 152–161, 164, and 165; (1) elongate (Fig. 163); (2) extremely elongate (Fig. 162).
60. *Female T7 with lateral margin*: (0) not emarginate (Figs. 152–157, 160–165); (1) emarginate (Figs. 158 and 159).

    The emargination is created by the extension of the lateral and posterior lamellae.
61. *Female T7 with apodemal region*: (0) forming an angle of roughly 45 degrees (Figs. 152–155, 157–159); (1) forming a right angle (Figs. 156, 160–165).
62. *Female T8 with cross bar extending from anterior ridge*: (0) absent (Figs. 147–149); (1) present, distinctly sclerotized (Figs. 150 and 151).
63. *Male S3 with setae at apex*: (0) not elongate, straight (or absent); (1) distinctly longer than those on apex of S2, straight; (2) distinctly longer than those on apex of S2, curved.

    There is the possibility that this character is developmentally linked with characters 64 and 65; however, they have been coded separately due to the fact that they vary independently.
64. *Male S4 with setae at apex*: (0) not elongate, straight (or absent); (1) distinctly longer than those on apex of S2, curved.
65. *Male S5 with setae at apex*: (0) not elongate, straight (or absent); (1) distinctly longer than those on apex of S2, straight; (2) distinctly longer than those on apex of S2, curved.
66. *Female S5*. (0) truncate or broadly rounded, with medioapical margin slightly or dramatically emarginate (except in *Brachynomada*, which has an autapomorphic medioapical projection); (1) elongate, with broadly trough-shaped with medioapical margin convex or forming posterior median point.
67. *Female S5 with apical margin*. (0) roughly in same plane as disk of S5; (1) forming ventrally directed lip.
68. *Female S6 with sclerotized area of disk*: (0) long, equal to or longer than processes (Figs. 2, 3, 5, 11–13); (1) reduced, much shorter than processes (except in *Bustes* where processes are not elongate; Figs. 4, 7, 9, 10)
69. *Female S6 with inner, apical margin between processes*: (0) convex (Fig. 13); (1) evenly concave or V-shaped (Figs. 11 and 12); (2) concave medially, with slight lateral convexity (i.e., sinuous; Fig. 7); (3) medially forming a straight line roughly perpendicular to inner margins of processes (Figs. 9 and 10)
70. *Female S6 with principal setae*: (0) absent (Fig.5); (1) stout, rounded to bluntly pointed (Figs. 11 and 12); (2) forming conical denticles (Fig. 13); (3) elongate, pointed, hooked (Figs. 7 and 10).
71. *Female S6 with principal setae directed*: (0) medioventrally to ventrally (Figs. 7 and 10–12); (1) laterally (Fig. 13).
72. *Female S6 with marginal setae*: (0) present along entire margin (Figs. 11–13); (1) absent on medial margin between apical lateral processes (Figs. 7, 9, and 10).
73. *Female S6 with apical margin of processes*: (0) not forming flat, apical plate (Fig. 13); (1) forming small, rounded, flat, apical plate (Figs. 11 and 12); (2) forming thin, pointed, stake like, usually three pronged, flat, apical plate (Fig. 7).
74. *Female S6 with differentiated external lateral series of long setae on processes*: (0) absent; (1) present (Figs. 2 and 7).

    I have coded *Hexepeolus* as not having a differentiated external series of long setae although it seems possible that some of the more basal setae in the series of stout apical setae might be homologous with the lateral series.
75. *Female S6 length (excluding apical setae) basal to mediolateral apodeme equaling approximately*: (0) 15% of total S6 length; (1) 30–40% of total S6 length; (2) 45–60% of total S6 length; (3) 80% of total S6 length.
76. *Female S6 with lateral membranous flap*: (0) absent (Fig. 7); (1) present, posterior margin of mediolateral apodeme not distinct from lateral margin of process (Fig. 2).
77. *Female S6 with inner margin of basal apodeme*: (0) membranous or weakly sclerotized (Fig. 13); (1) heavily sclerotized along majority of length (Fig. 7).
78. *Female S6 with inner basal margin, near mediolateral apodeme*: (0) not clearly meeting outer margin (Figs. 11 and 12); (1) distinctly meeting outer margin, forming sclerotized V or U shape (Figs. 7 and 13).
79. *Female S6 with digitiform appendage of basal apodeme*: (0) absent (Fig. 2); (1) present, strongly protruding (Fig.7); (2) present, weakly protruding (Fig. 22B).
80. *Female S6 with digitiform appendage of basal apodeme*: (0) attached sub-basally, widely mesad main basal apodeme (Fig. 11); (1) attached sub-basally, proximal to main basal apodeme (Fig. 7); (2) attached basally, apparently brought into close proximity of basal apodeme by way of a crease or fold in the integument between the apodeme and appendage (Fig. 13).

    Character state 2 is found in many *Epeolus*. It seems likely that this appendage is homologous to those found in other epeolines due to the observation that the appendage is not folded next to the apodeme in *Epeolus lectoides* (Fig. 8).
81. *Female S6 with basolateral sclerotic band of disk*: (0) absent (Fig. 7); (1) present (Fig. 2).
82. *Male S7 with distinct distal process*: (0) absent, lacking medial constriction forming process (Figs. 56–58); (1) present (Fig. 16).
83. *Male S7 with apical, median emargination*: (0) absent (Figs. 56 and 57); (1) present (Fig. 16).
84. *Male S7 with apical, sublateral emarginations*: (0) absent (Figs. 64–67); (1) present (Fig. 16).
85. *Male S7 with apices of lateral lobes on distal process*: (0) beyond interlobal area (Fig. 68); (1) not extending as far as interlobal area (Fig. 81).
86. *Male S7 with lateral margins of distal process*: (0) roughly straight, parallel sided (Fig. 77); (1) roughly straight, widest basally (Fig. 64); (2) roughly straight, widest apically (Fig. 67); (3) rounded, giving plate a circular appearance (Fig. 79).
87. *Male S7 with setae along lateral margins of distal process*: (0) absent or sparse (Fig. 85); (1) numerous, primarily simple (Fig. 82); (2) numerous, primarily branched (Fig. 64).

    The long setae found in *Rhogepeolus* are especially branched. The branched nature of the setae is difficult to observe without use of a compound microscope.
88. *Male S7 with setae in distinct pocket formed in emargination near lateral lobe on ventral surface of distal process*: (0) absent; (1) present (Figs. 86–95).
89. *Male S7 with setae on dorsal surface of lateral lobes of distal process*: (0) absent; (1) present (Figs. 68–76).
90. *Male S8 with distinct lateral apodemes*: (0) absent (Fig. 63); (1) short, rounded (Fig. 62); (2) long, angular (Figs. 59 and 96); (3) long, rounded (Figs. 98 and 99).

91. *Male S8 with medioapical process*: (0) absent (Fig. 59); (1) clearly defined (Fig. 17).
92. *Male S8 with sides of medioapical process*: (0) not emarginate (Fig. 17); (1) emarginate medially (Figs. 114–118); (2) feebly emarginate apically (Figs. 107 and 108).
93. *Male ventral gonocoxite with prominent lobe on inner surface*: (0) absent; (1) present (Fig. 136).
94. *Male gonocoxite with median ventral margin*: (0) approximately straight or gently sloping (Fig. 135); (1) distinctly emarginate (Fig. 137).
95. *Gonostylus*: (0) simple, composed of a single structure (Fig. 128B); (1) composed of a single elongate process that is angled basally into a lobe (Fig. 129); (2) composed of two distinct, elongate processes (Fig. 130).
96. *Penis valves with dorsal connecting bridge*: (0) not discernable; (1) expanded into spatha; (2) roughly triangular; (3) roughly bar shaped.

    There is a marked tendency for *Doeringiella* and *Triepeolus* (but not *Triepeolus epeolurus*, *Triepeolus heterurus*, or old world *Triepeolus*) to have an elongate dorsal bridge relative to other epeolines in which this structure is bar shaped; however, intergradation made coding of distinct character states difficult.
97. *Penis valves with dorsal connecting bridge*: (0) well sclerotized; (1) poorly sclerotized.
98. *Penis valve with dorsobasal lobe*: (0) absent; (1) present, not conspicuously covering basolateral margins of penis; (2) present, conspicuously covering basolateral margins of penis.
99. *Penis and penis valve with articulating surfaces*: (0) curved; (1) highly recurved, scroll-like (Fig. 145).
100. *Penis valve*: (0) lacking inner, medial projection; (1) with inner, medial projection (Fig. 131).
101. *Penis with small lamellate projection on dorsolateral margin*: (0) absent (Fig. 144); (1) present medially (Fig. 145); (2) present subapically (Fig. 143).
102. *Penis with widely divergent, fleshy lobe on lateral margin*: (0) absent; (1) present (Fig. 141).

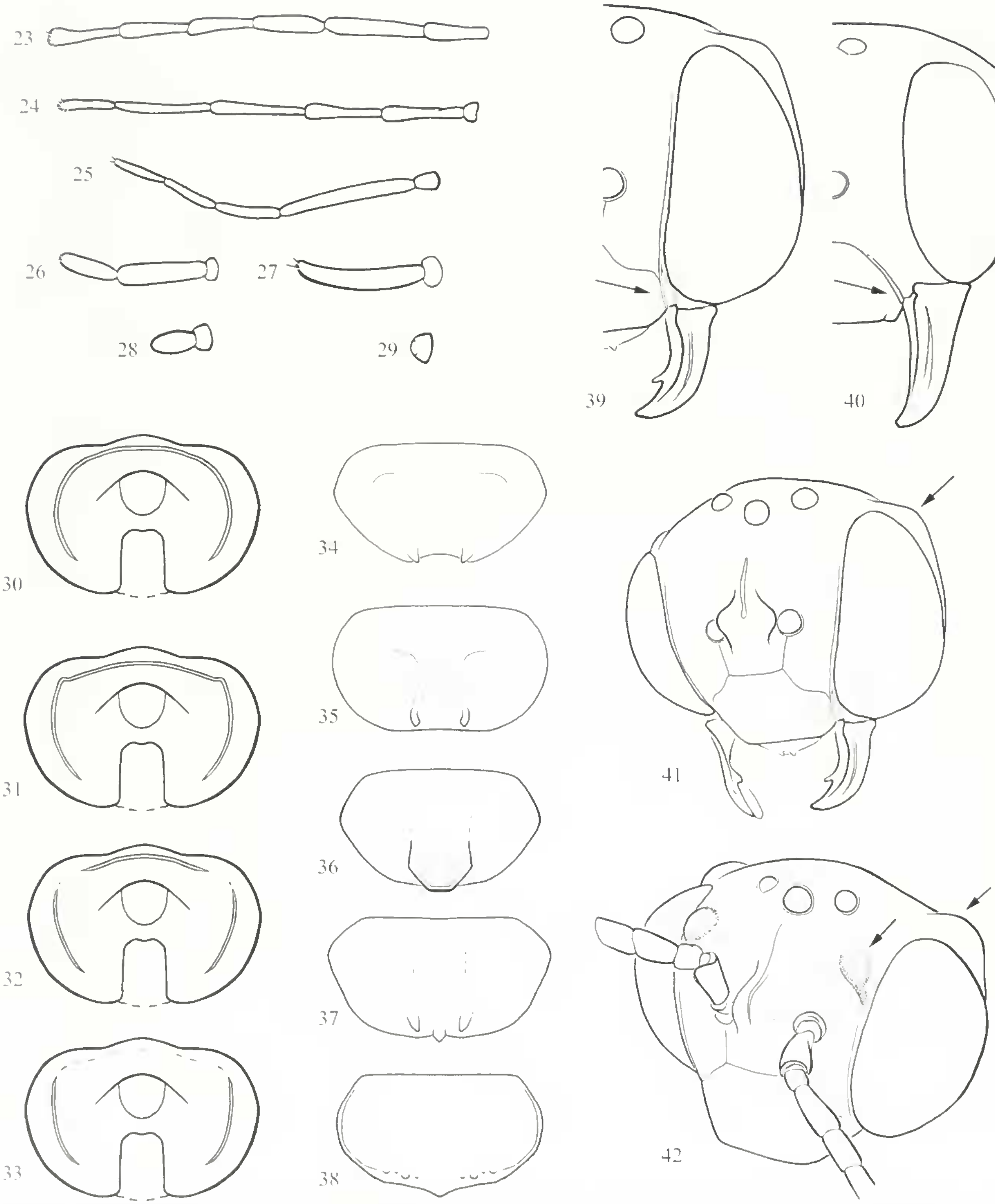
APPENDIX 3. Data matrix of morphological character states. - = not applicable; + = multistate (in both cases 2,3).

Characters 1-51

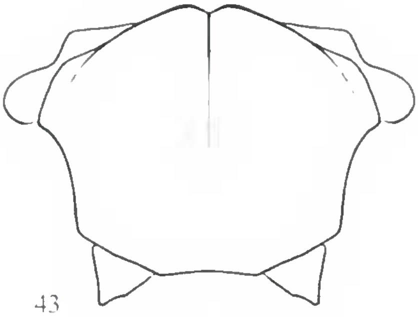
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Biastes	0	4	1	0	0	0	0	1	0	1	2	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	-	0	1	1	1	1	0	2	0	0	0	2	1	1	0	0	0	1	0
Brachynomada	0	4	1	0	0	0	0	0	0	1	1	1	3	0	0	1	1	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	-	0	1	1	1	1	0	0	0	0	0	2	0	0	0	2	1	1	0
Hexepeolus	1	5	1	0	2	0	1	2	0	1	2	1	3	0	0	0	1	1	0	0	0	0	0	2	1	1	1	0	0	0	0	0	-	0	1	1	0	0	1	2	0	0	1	0	0	0	2	2	1	1	0
Holcopasites	0	5	1	0	0	0	1	1	0	1	2	1	2	0	0	0	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	-	0	1	0	1	0	0	2	0	0	0	2	1	1	0	1	0	1	0
Nomada	0	5	1	0	2	0	0	0	0	0	1	0	3	0	0	0	1	1	0	0	0	0	1	2	0	0	2	0	0	0	0	0	-	0	2	1	0	1	1	0	0	0	1	0	1	1	0	0	0	1	0
R. bigibbosus	1	+	0	1	1	1	1	1	0	2	2	1	3	0	0	1	0	1	0	0	0	1	1	2	0	0	2	0	0	0	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	2	0	2	1	2	1
R. emarginatus	1	2	0	1	0	1	0	3	0	2	2	1	3	0	0	1	0	1	0	0	0	1	2	2	0	0	2	0	0	0	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	2	0	1	1	2	1
O. armata	1	0	1	1	1	1	1	1	1	2	0	0	2	0	0	1	1	0	0	0	0	1	1	2	0	0	2	0	1	0	0	1	1	0	2	1	1	1	0	0	1	0	1	0	0	1	0	0	0	2	0
O. batesi	1	1	1	1	1	1	1	1	1	2	0	0	3	0	0	1	1	0	0	0	0	1	1	2	0	0	2	0	0	0	0	1	1	0	2	1	1	0	0	0	1	0	1	0	0	1	0	0	1	2	1
Thalestria	1	1	0	1	1	0	1	2	1	2	0	0	2	0	1	1	1	0	0	0	1	1	1	2	0	0	2	0	2	0	0	1	0	1	0	0	0	0	1	1	1	1	1	2	2	1	0	1	1	1	0
Rhinepeolus	1	1	0	1	1	0	0	3	0	2	1	1	3	0	0	1	0	1	0	0	1	1	2	1	1	0	0	0	2	0	0	1	0	2	1	0	0	0	1	0	1	0	1	2	2	2	1	2	1	0	0
D. bizonata	1	1	0	1	2	0	1	2	0	2	1	1	3	1	1	1	0	2	0	0	3	1	1	2	0	2	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	1	2	2	2	2	2	1	1	0
D. cingillata	1	+	0	1	2	0	1	2	0	2	1	1	3	1	1	1	0	1	0	0	3	1	1	2	0	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	2	2	2	2	2	1	1	0
D. crassicornis	1	1	0	1	2	0	1	2	0	2	1	1	3	1	1	1	0	1	0	0	2	1	0	2	0	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	2	2	2	2	2	1	1	0
D. crinita	1	1	0	1	2	0	1	2	0	2	1	1	3	1	1	1	0	1	0	0	2	1	0	2	0	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	2	2	2	2	2	1	1	0
D. holmbergi	1	1	0	1	2	0	1	2	0	2	1	1	3	1	1	1	0	1	0	0	3	1	1	2	0	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	2	2	2	2	2	1	1	0
Pseudepeolus	1	1	0	1	2	0	1	2	0	2	0	1	1	0	0	1	0	1	0	0	3	1	2	1	0	0	2	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	2	2	2	1	2	1	1	0
T. ancoratus	1	3	0	1	0	0	1	2	0	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	1	2	2	0	2	1	0	0
T. distinctus	1	2	0	1	1	0	1	2	0	2	1	0	2	0	0	1	0	1	0	0	3	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	1	2	0	2	1	1	0
T. epeolurus	1	2	0	1	3	0	1	2	0	2	0	1	3	0	0	1	0	1	0	0	3	1	2	1	0	2	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	2	2	2	1	2	1	1	0
T. heterurus	1	2	0	1	2	0	1	2	0	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	0	2	1	2	0
T. kathrynae	1	2	0	1	0	0	1	2	0	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	2	1	2	0	2	1	2	0
T. lunatus	1	3	0	1	0	0	1	2	1	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	0	2	1	0	0
T. nobilis	1	1	0	1	0	0	1	2	0	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	0	2	1	0	0
T. quadrifasciatus	1	3	0	1	2	0	1	1	0	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	0	2	1	1	0
T. tristis	1	3	0	1	1	0	1	2	0	2	1	0	2	0	0	1	0	1	0	0	3	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	2	2	2	1	2	1	1	0
T. ventralis	1	3	0	1	0	0	1	2	0	2	1	0	2	0	0	1	0	1	0	0	3	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	1	2	1	1	0
T. vicinus	1	3	0	1	0	0	1	2	1	2	0	0	2	0	0	1	0	1	0	0	4	1	2	1	0	2	2	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	0	2	1	1	0
E. compactus	1	1	0	1	2	1	1	2	0	2	1	1	2	0	0	1	0	2	0	1	3	1	2	1	0	1	2	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	2	2	0	2	1	0	0
E. lectoides	1	1	0	1	1	0	1	2	0	2	1	0	1	0	0	1	0	2	1	1	3	1	2	1	0	2	1	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	1	2	2	0	2	1	0	0
E. mesillae	1	1	0	1	1	1	1	2	0	2	1	1	1	0	0	1	0	2	0	0	3	1	1	2	0	2	1	0	0	0	0	1	0	2	1	0	0	0	1	1	1	0	1	1	2	1	0	2	1	1	0
E. natalensis	1	2	0	1	2	1	1	4	0	2	1	1	2	0	0	1	0	1	0	1	3	1	2	2	0	0	2	0	0	0	0	1	2	1	1	0	0	0	1	1	1	0	1	1	2	2	0	2	1	1	0
E. schummeli	1	1	0	1	2	1	1	2	0	2	1	1	2	0	0	1	0	2	0	1	3	1	2	1	0	0	2	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	2	2	2	0	2	1	0	0
E. t. rozenburgensis	1	1	0	1	2	1	1	4	0	2	1	1	1	0	0	1	0	2	0	1	3	1	2	2	0	2	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	2	2	0	2	1	0	0
E. bifasciatus	1	1	0	1	2	1	1	2	0	2	1	1	1	0	0	1	0	1	2	2	3	0	2	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	1	2	2	0	2	1	1	0
E. variolosus	1	1	0	1	1	1	1	2	0	2	1	1	0	0	0	1	0	2	2	2	3	0	2	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	2	2	0	2	1	1	0

Characters 52-102

	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102
Biastes	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	3	0	0	0	0	-	0	0	0	0	-	-	-	-	-	1	1	0	0	0	0	1	1	1	0	0	0	0
Brachynomada	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	-	0	1	1	2	0	1	0	0	-	0	1	1	0	-	2	0	0	0	2	1	0	1	0	2	1	0	0	0	0	0	0
Hexepeolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	1	0	-	1	0	1	0	-	-	-	-	-	2	0	-	0	0	0	1	0	1	0	0	0	0
Holcopasites	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	2	1	1	1	0	-	1	0	0	0	-	-	-	-	-	0	0	-	0	0	0	0	-	0	0	0	0	0
Nomada	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	2	1	1	0	0	-	1	0	0	0	-	-	-	-	-	2	1	0	0	0	0	4	0	0	0	0	0	0
R. bigibbosus	0	0	1	0	1	3	0	0	1	0	0	2	1	0	1	0	0	1	1	0	0	1	1	2	0	0	0	1	0	0	1	1	0	-	1	2	0	0	2	1	0	0	0	0	1	0	1	0	1	0	0
R. emarginatus	0	0	1	0	1	3	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	1	1	2	0	0	0	1	0	0	1	1	0	-	0	2	0	0	2	1	0	0	0	0	1	0	1	0	1	0	0
O. armata	0	1	1	0	0	4	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	2	0	0	0	1	0	0	1	1	0	-	2	2	0	0	3	1	0	0	0	0	1	0	1	0	1	0	0
O. batesi	0	1	1	0	1	4	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	2	0	0	0	1	0	0	1	1	0	-	2	2	0	0	3	1	0	0	0	0	1	0	1	0	1	0	0
Thalestria	0	0	0	0	0	1	0	2	0	1	1	0	0	2	1	0	1	3	3	0	1	2	1	0	0	0	1	0	-	0	1	1	1	0	0	0	0	0	2	1	0	0	0	0	2	0	2	0	1	2	0
Rhinepeolus	0	0	0	0	0	5	0	0	0	1	1	2	1	2	1	1	1	2	3	0	1	2	1	1	0	1	0	0	-	0	1	1	1	1	0	0	0	0	2	1	0	0	0	0	3	0	2	0	1	0	0
D. bizonata	0	0	0	0	0	5	0	1	0	1	1	2	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	2	1	1	0	1	0	3	0	2	1	1	0	0
D. cingillata	0	0	0	1	0	5	0	1	0	1	1	2	1	1	1	1	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	2	1	1	1	1	0	3	0	2	1	1	1	0
D. crassicornis	0	0	0	1	0	5	0	1	0	1	1	2	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	0	1	0	0	2	1	1	1	1	0	3	0	2	1	1	1	0
D. crinita	0	0	0	1	0	5	0	1	0	1	1	2	1	2	1	1	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	1	0	0	2	1	1	1	1	0	3	0	2	1	1	1	0
D. holmbergi	0	0	0	1	0	5	0	1	0	1	1	2	1	1	1	1	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	2	1	1	1	1	0	3	0	2	1	1	0	0
Pseudepeolus	0	0	0	0	0	5	0	0	0	1	1	1	1	1	1	0	1	2	3	0	1	2	1	1	0	1	0	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. ancoratus	0	0	0	1	0	5	1	1	0	1	1	0	1	2	1	1	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. distinctus	0	0	0	0	1	5	0	1	0	1	1	0	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	2	1	0	1	0	1	1	0	0	1	0	2	1	1	0	1	0	3	0	2	0	1	0	0
T. epeolurus	2	0	0	0	1	5	1	0	0	1	1	0	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	2	1	0	1	1	1	1	0	0	1	0	2	1	1	0	1	0	3	0	2	0	1	0	0
T. heterurus	0	0	1	0	0	5	0	1	0	1	1	0	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. kathrynae	0	0	0	0	1	5	0	1	0	1	1	0	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	2	1	0	1	1	1	1	0	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. lunatus	0	0	0	1	1	5	1	1	0	1	1	0	1	2	1	1	1	3	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. nobilis	0	0	0	1	0	5	0	1	0	1	1	0	1	2	1	0	1	3	3	0	1	2	1	1	0	1	1	1	1	0	1	0	1	1	3	1	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. quadrifasciatus	0	0	0	1	1	5	0	1	0	1	1	0	1	2	1	1	1	3	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
T. tristis	0	0	0	0	0	5	1	0	0	1	1	2	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	2	1	0	0	0	0	3	0	2	0	1	0	0
T. ventralis	0	0	0	0	1	5	1	0	0	1	1	2	1	2	1	0	1	2	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	0	0	3	0	2	0	1	2	0
T. vicinus	0	0	0	1	1	5	1	1	0	1	1	0	1	2	1	1	1	3	3	0	1	2	1	1	0	1	1	1	1	0	1	1	1	1	3	0	1	0	2	1	0	0	1	0	3	0	2	0	1	0	0
E. compactus	1	0	0	0	0	2	0	0	1	0	0	0	1	2	1	0	0	0	2	1	0	0	1	2	0	0	1	1	2	0	1	0	1	0	0	0	0	1	2	1	0	0	0	1	3	0	1	0	1	0	1
E. lectoides	1	0	0	0	0	2	0	0	1	0	1	0	1	2	1	0	0	0	2	1	0	0	1	2	0	0	1	1	1	0	1	0	1	0	0	0	0	1	2	1	2	0	0	1	3	1	1	0	1	0	1
E. mesillae	1	0	0	0	0	2	0	0	1	0	0	1	1	2	1	0	0	0	2	1	0	0	1	2	0	0	0	0	-	0	1	0	1	0	0	0	0	1	2	1	0	0	0	1	3	0	1	0	1	0	1
E. natalensis	1	0	0	0	0	2	0	0	1	0	0	0	1	2	1	0	0	0	2	1	0	0	1	2	0	1	1	1	2	0	1	0	1	0	0	0	0	1	2	1	0	0	0	1	3	0	1	0	1	0	1
E. schummeli	1	0	0	0	0	2	0	0	1	0	0	0	1	2	1	0	0	0	2	1	0	0	1	2	0	0	1	1	2	0	1	0	1	0	0	0	0	1	2	1	2	0	0	1	3	0	1	0	1	0	1
E. t. rozenburgensis	1	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	2	1	0	0	1	2	0	0	1	0	-	0	1	0	1	0	0	0	0	1	2	1	0	0	0	1	3	1	1	0	1	0	1
E. bifasciatus	1	0	0	0	0	2	0	0	1	0	0	0	1	2	1	0	0	0	2	1	0	0	1	2	0	0	1	2	2	0	1	0	1	0	0	0	0	1	2	1	2	0	0	1	3	0	1	0	1	0	0
E. variolosus	1	0	0	0	0	2	0	0	1	0	0	1	1	2	1	0	0	0	2	1	0	0	1	2	0	0	1	0	-	0	1	0	0	0	0	0	0	1	2	1	2	0	0	1	3	0	1	0	1	0	0



Figs. 23–29. Maxillary palpi of Nomadinae. 23. *Hexepeolus rhodogyne*. 24. *Nomada pampicola*. 25. *Brachynomada scotti*. 26. *Triepeolus lunatus*. 27. *Triepeolus kathrynae*. 28. *Odyneropsis batesi*. 29. *Odyneropsis armata*. Figs. 30–33. Diagrammatic view of posterior surfaces of head capsules, showing various character-states of the preoccipital carina; redrawn from Roig-Alsina (1989). See character 21, Appendix 2 for further details. Figs. 34–38. Labra of Nomadinae. 34. *Triepeolus distinctus*. 35. *Triepeolus kathrynae*. 36. *Triepeolus epeolurus*. 37. *Pseudepeolus fasciatus*. 38. *Nomada pampicola*. Figs. 39 and 41. *Epeolus tarsalis rozenburgensis*, oblique view of head capsule. 39. Arrow pointing to lateroclypeal carina. 41. Arrow pointing to dorsal protrusion of gena. Fig. 40. *Hexepeolus rhodogyne*, arrow pointing to lateroclypeal carina. Fig. 42. *Epeolus variolosus*, arrows pointing to dorsal protrusion of gena and glabrous lobe near compound eye.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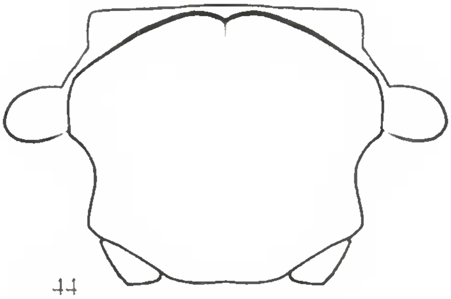
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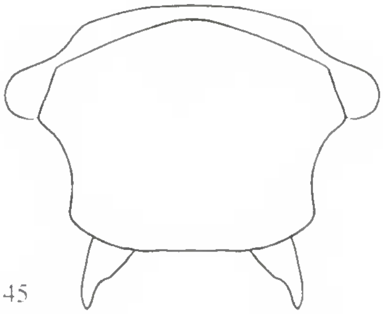
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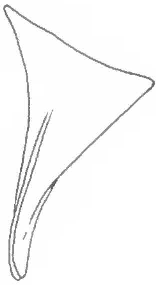
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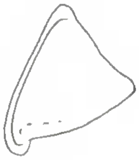
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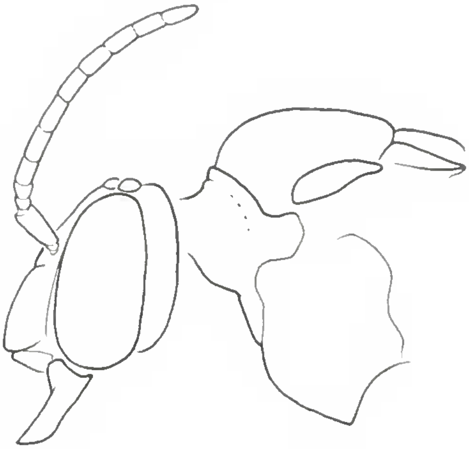
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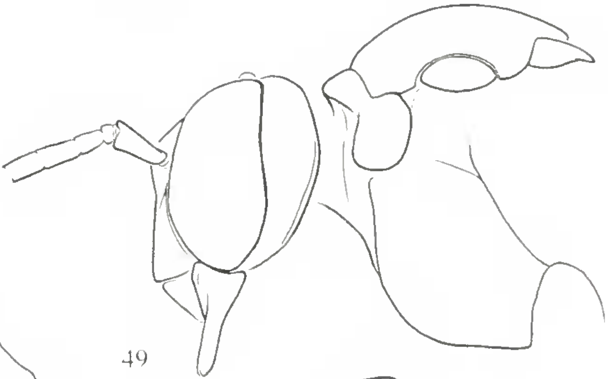
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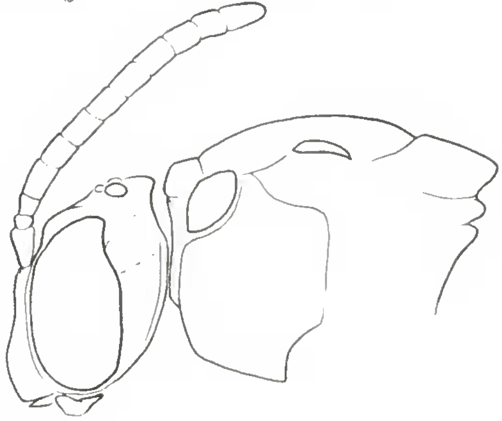
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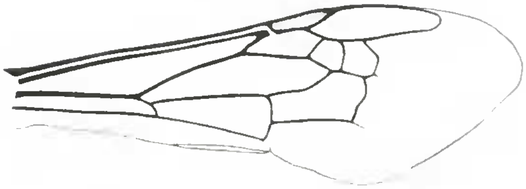
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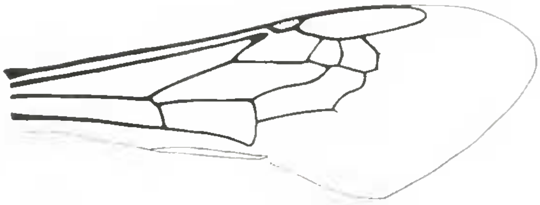
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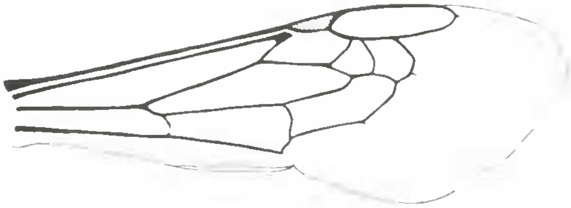
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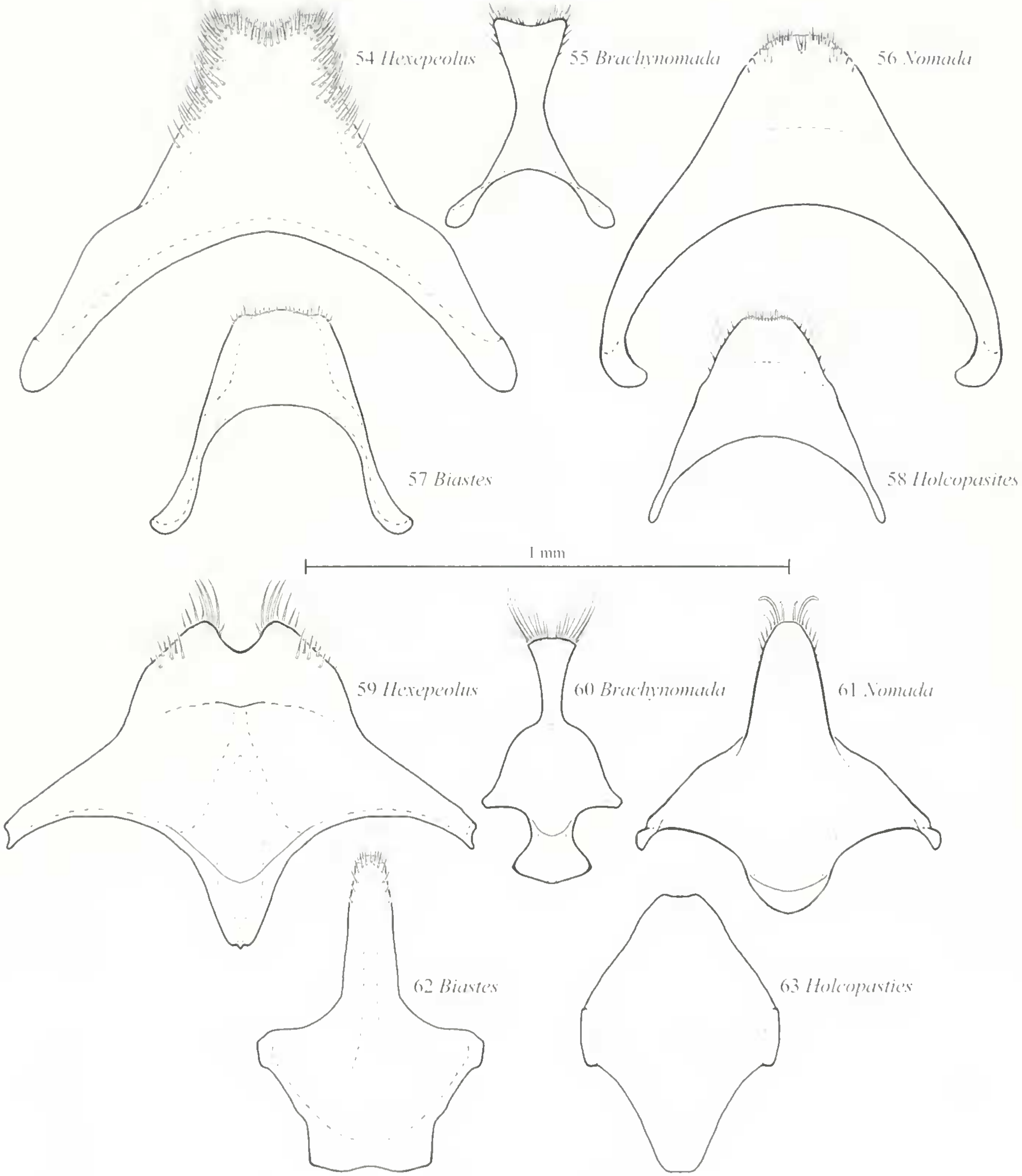
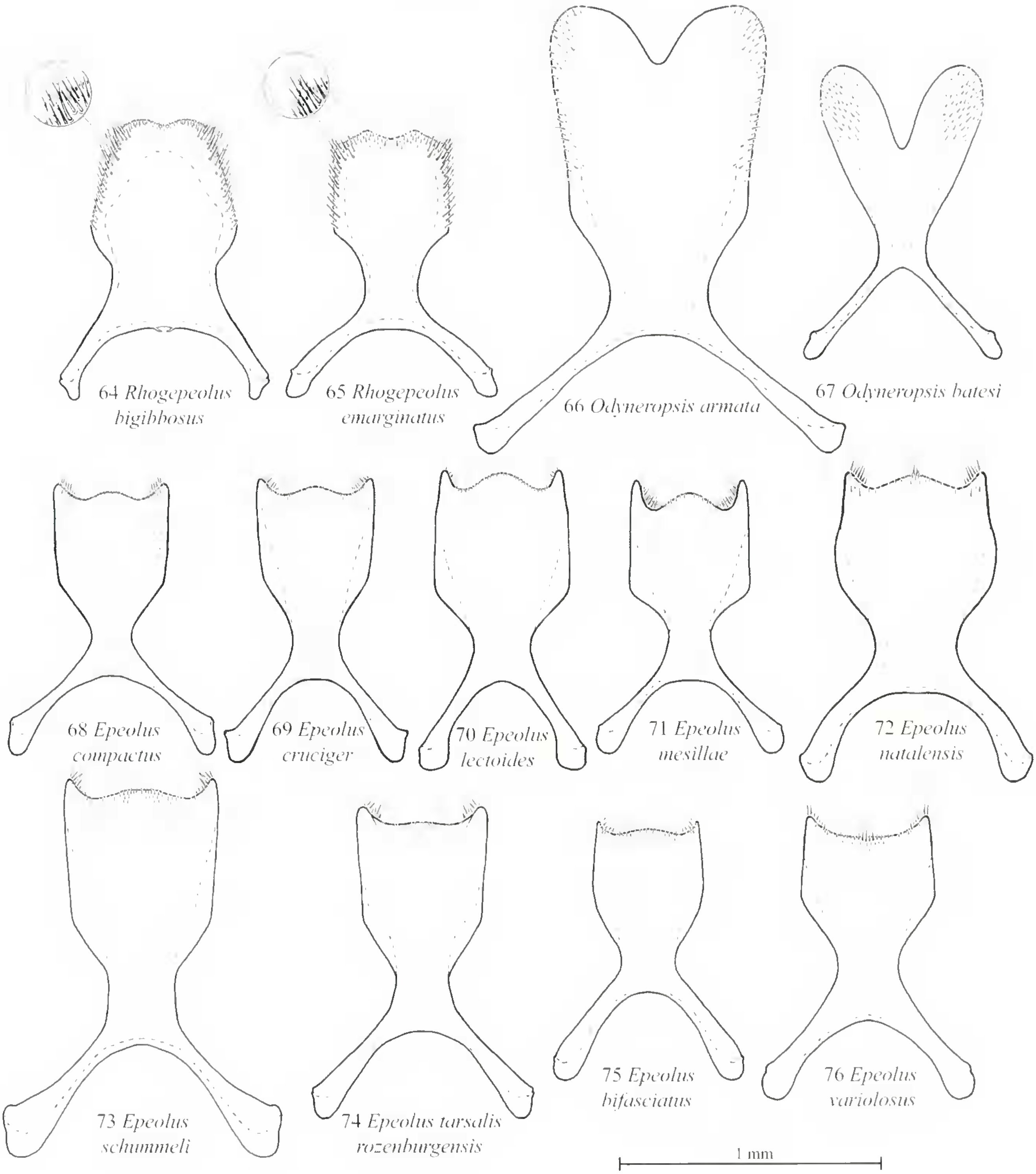
Figs. 43–45. Dorsal surfaces of pronota, scuta, and axillae. 43. *Doeringiella crassicornis*. 44. *Nomada pampicola*. 45. *Triepeolus quadrifasciatus*. Figs. 46 and 47. Axillar spines. 46. *Odyneropsis armata*. 47. *Epeolus natalensis*. Figs. 48–50. Lateral view of heads and mesosomata. 48. *Odyneropsis batesi*. 49. *Triepeolus kathrynae*. 50. *Epeolus bifasciatus*. Figs. 51–53. Forewings. 51. *Odyneropsis armata*. 52. *Thalestria spinosa*. 53. *Triepeolus quadrifasciatus*.



Figs. 54–58. Ventral view of male seventh sterna. Figs. 59–63. Ventral view of male eighth sterna. See Table 3 for species names.


64 *Rhogepeolus bigibbosus*

65 *Rhogepeolus emarginatus*

66 *Odyneropsis armata*

67 *Odyneropsis batesi*

68 *Epeolus compactus*

69 *Epeolus cruciger*

70 *Epeolus lectoides*

71 *Epeolus mesillae*

72 *Epeolus natalensis*

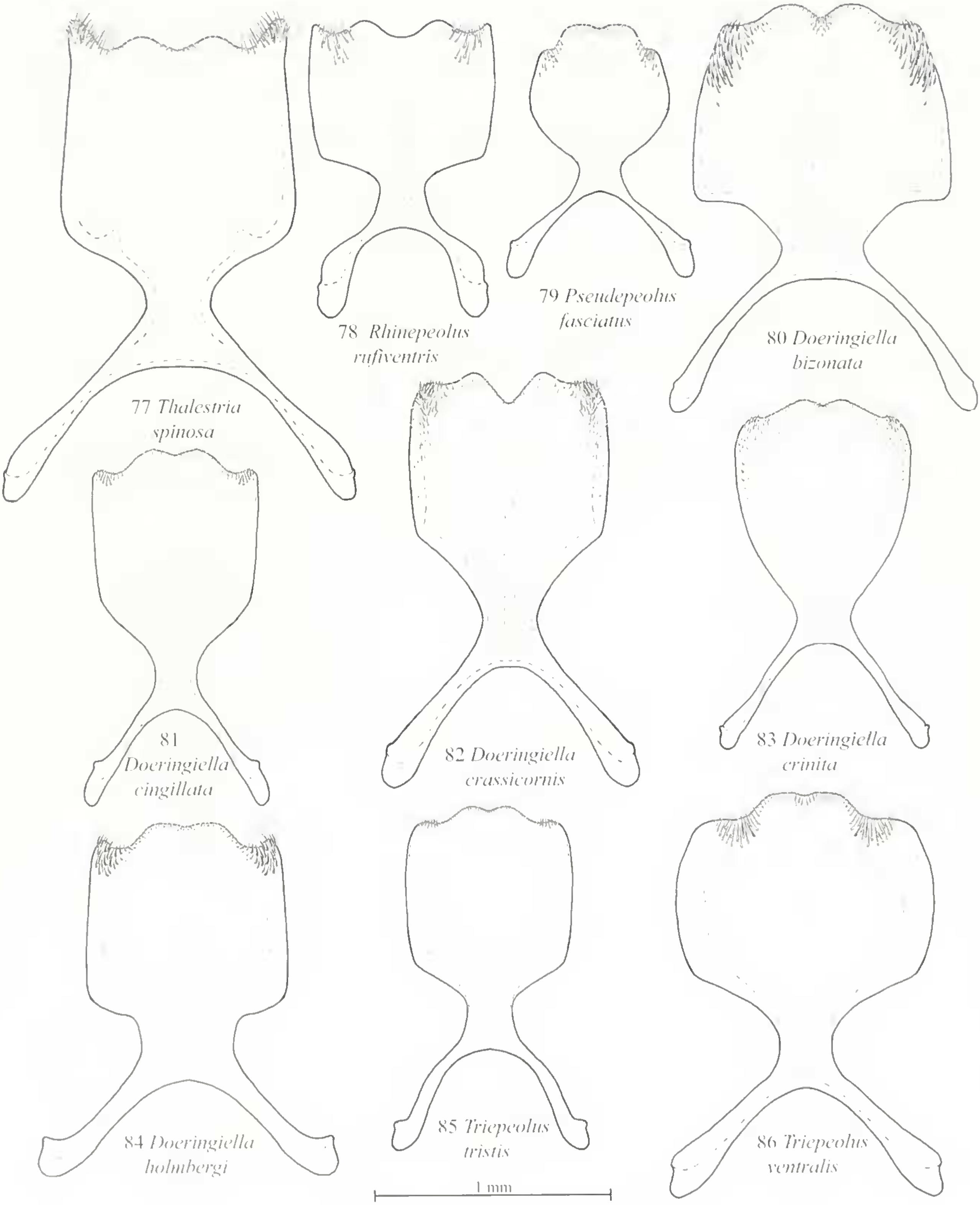
73 *Epeolus schummeli*

74 *Epeolus tarsalis rozenburgensis*

75 *Epeolus bifasciatus*

76 *Epeolus variolosus*

Figs. 64–76. Ventral view of male seventh sterna.



77 *Thalestria spinosa*

78 *Rhinepeolus rufiventris*

79 *Pseudepeolus fasciatus*

80 *Doeringiella bizonata*

81 *Doeringiella cingillata*

82 *Doeringiella crassicornis*

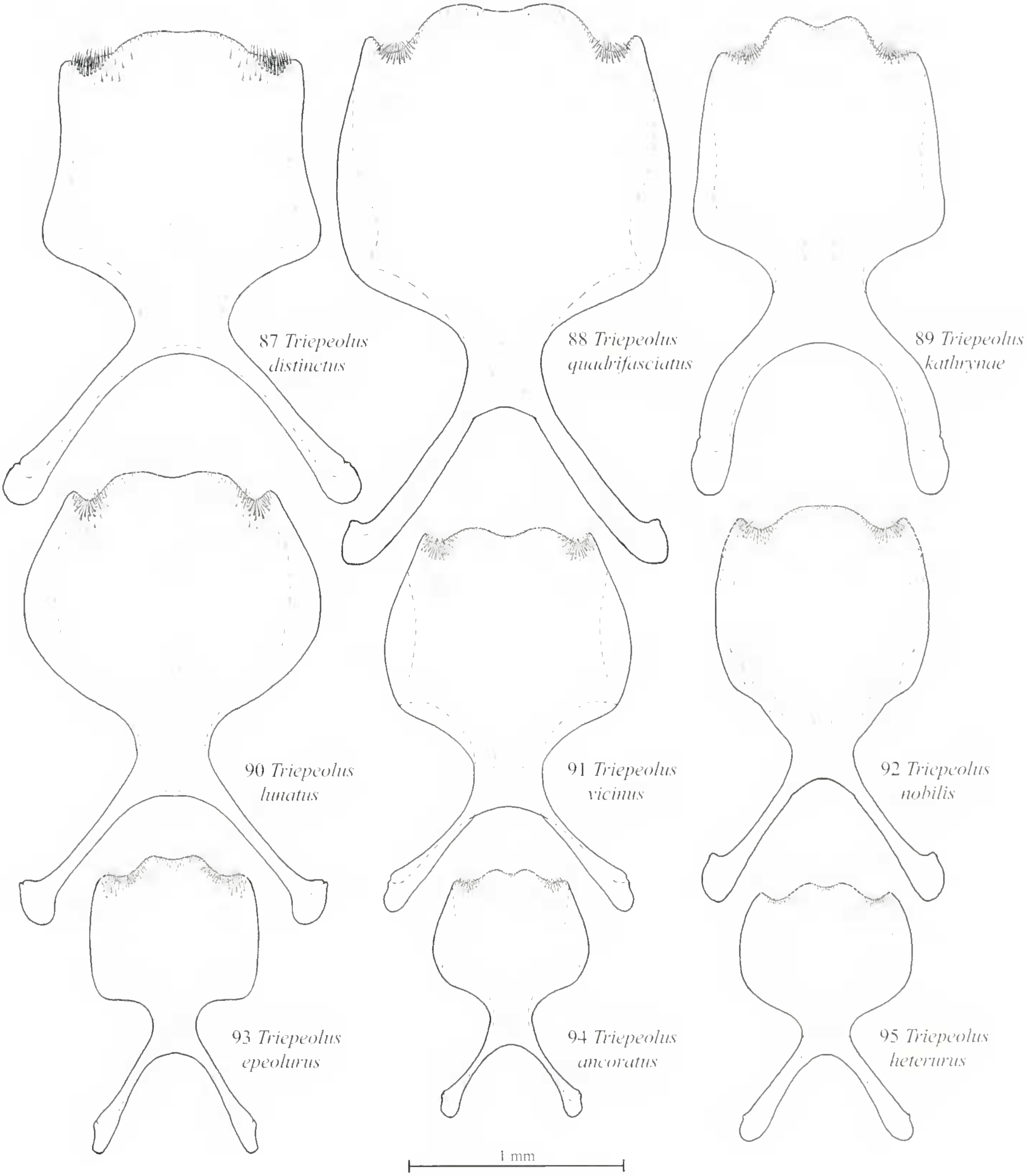
83 *Doeringiella crinita*

84 *Doeringiella holmbergi*

85 *Triepeolus tristis*

86 *Triepeolus ventralis*

Figs. 77–86. Ventral view of male seventh sterna.



87 *Triepeolus distinctus*

88 *Triepeolus quadrifasciatus*

89 *Triepeolus kathrynae*

90 *Triepeolus lunatus*

91 *Triepeolus vicinus*

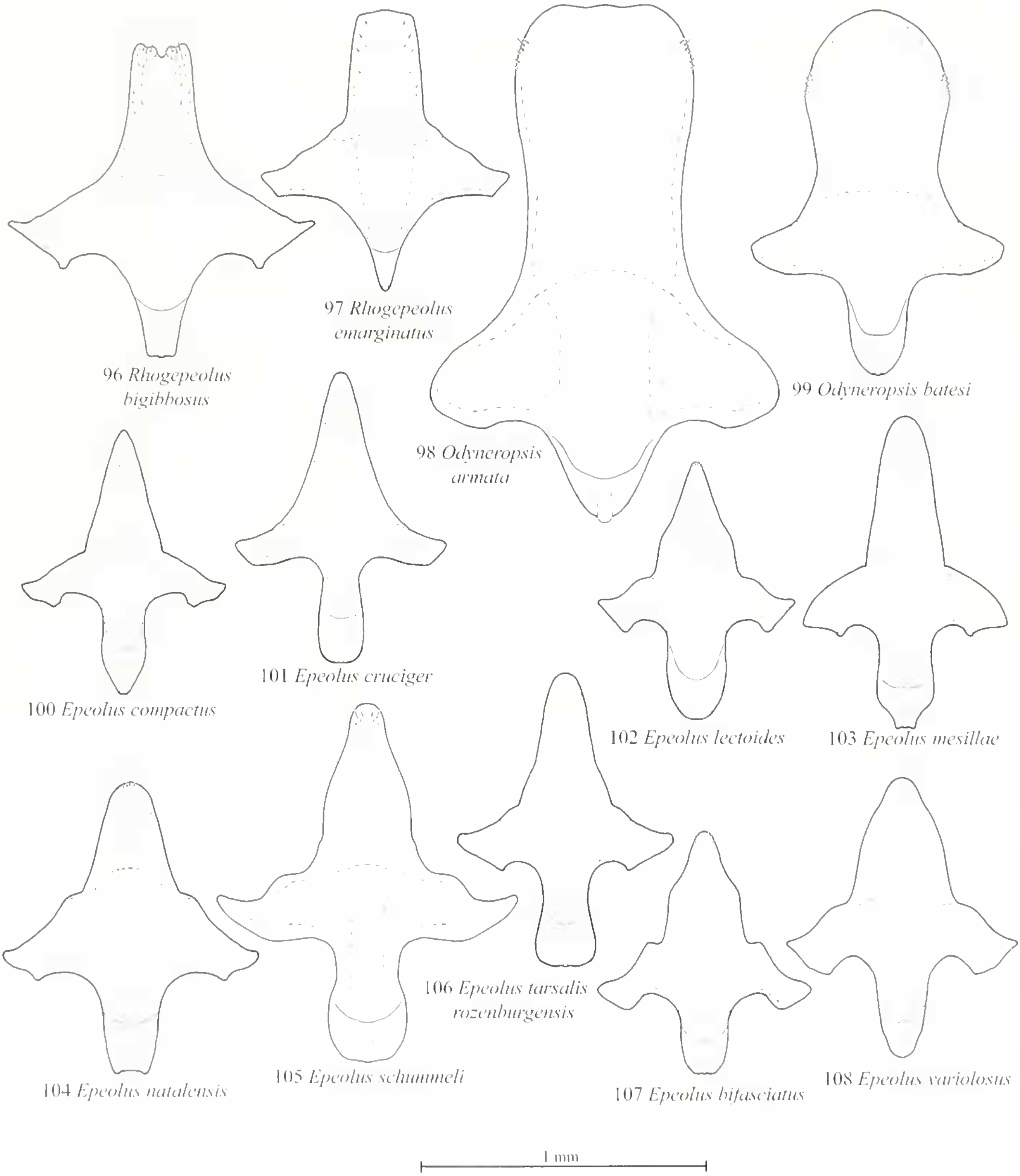
92 *Triepeolus nobilis*

93 *Triepeolus epeolurus*

94 *Triepeolus ancoratus*

95 *Triepeolus heterurus*

Figs. 87–95. Ventral view of male seventh sterna.


96 *Rhogepeolus bigibbosus*

97 *Rhogepeolus emarginatus*

98 *Odyneropsis armata*

99 *Odyneropsis batesi*

100 *Epeolus compactus*

101 *Epeolus cruciger*

102 *Epeolus lectoides*

103 *Epeolus mesillae*

104 *Epeolus natalensis*

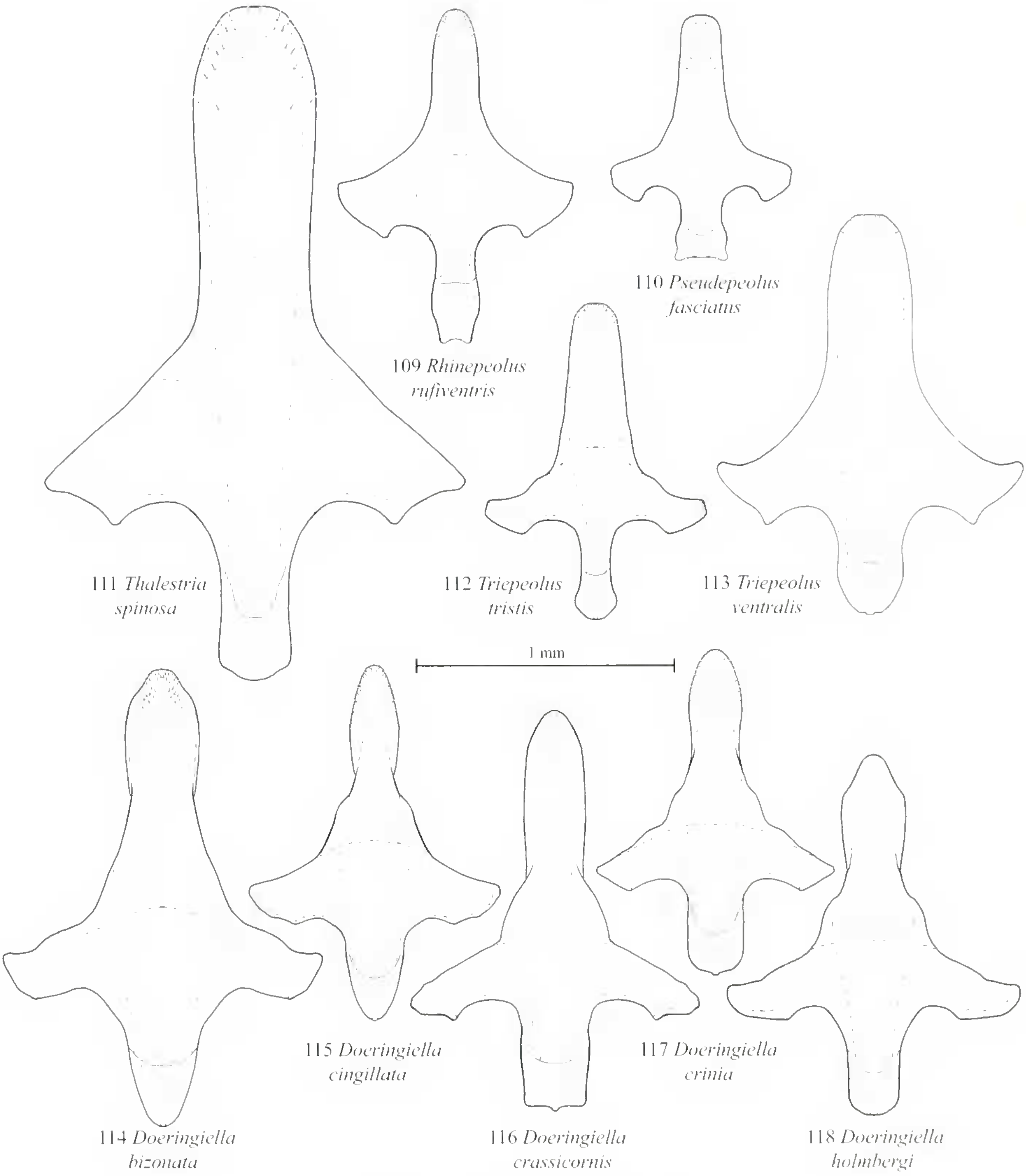
105 *Epeolus schummeli*

106 *Epeolus tarsalis rozenburgensis*

107 *Epeolus bifasciatus*

108 *Epeolus variolosus*

Figs. 96–108. Ventral view of male eighth sterna.



109 *Rhinepeolus rufiventris*

110 *Pseudepeolus fasciatus*

111 *Thalestria spinosa*

112 *Triepeolus tristis*

113 *Triepeolus ventralis*

114 *Doeringiella bizonata*

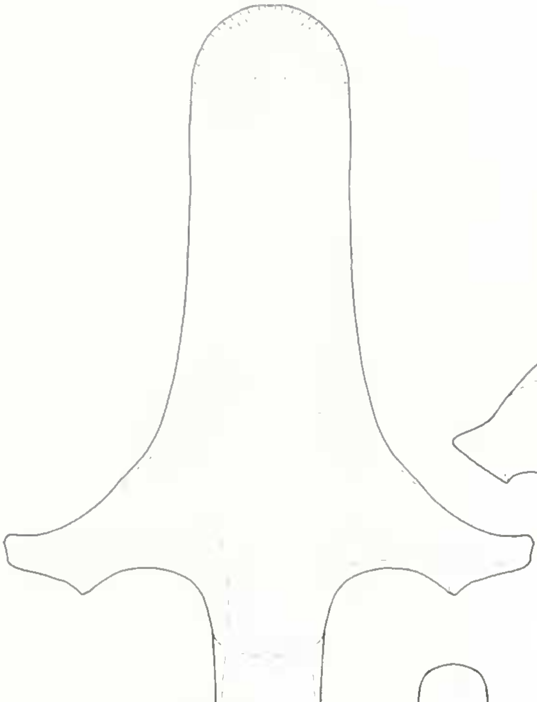
115 *Doeringiella cingillata*

116 *Doeringiella crassicornis*

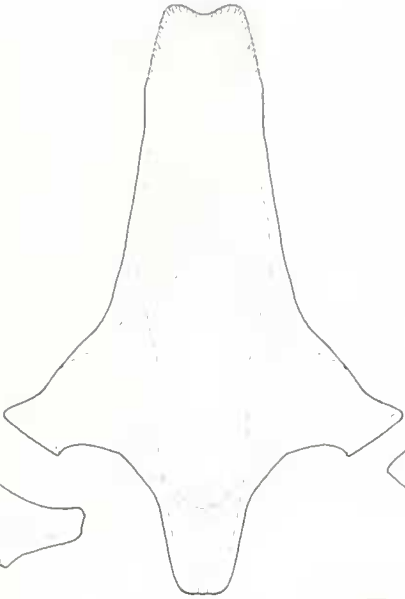
117 *Doeringiella crinia*

118 *Doeringiella holmbergi*

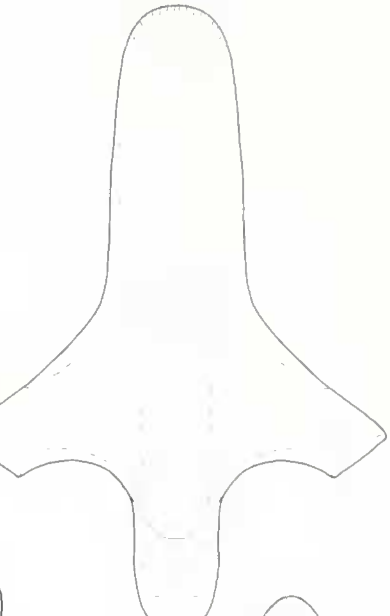
Figs. 109–118. Ventral view of male eighth sterna.



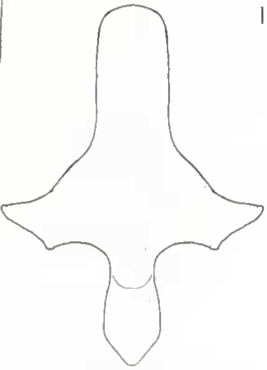
119 *Triepeolus quadrifasciatus*



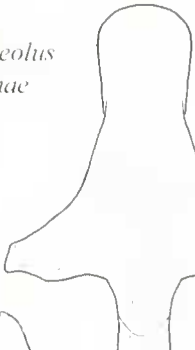
120 *Triepeolus kathrynae*



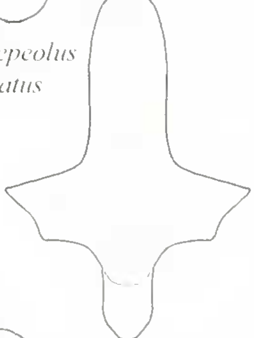
121 *Triepeolus lunatus*



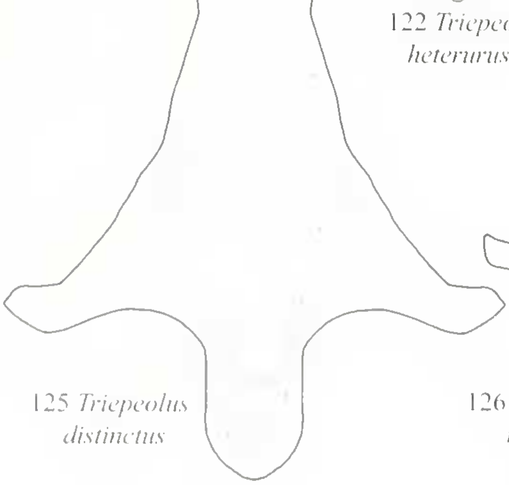
122 *Triepeolus heterurus*



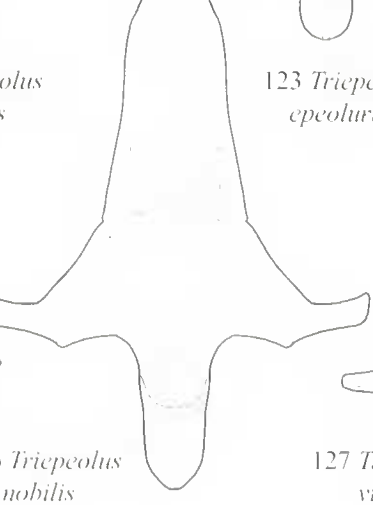
123 *Triepeolus epeolurus*



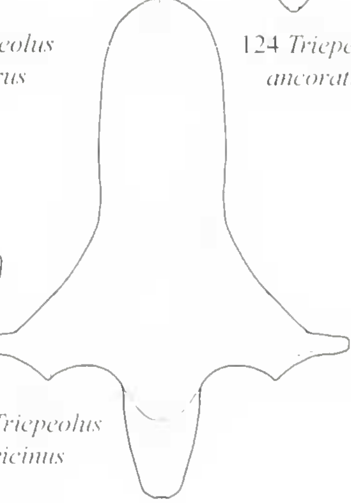
124 *Triepeolus ancoratus*



125 *Triepeolus distinctus*



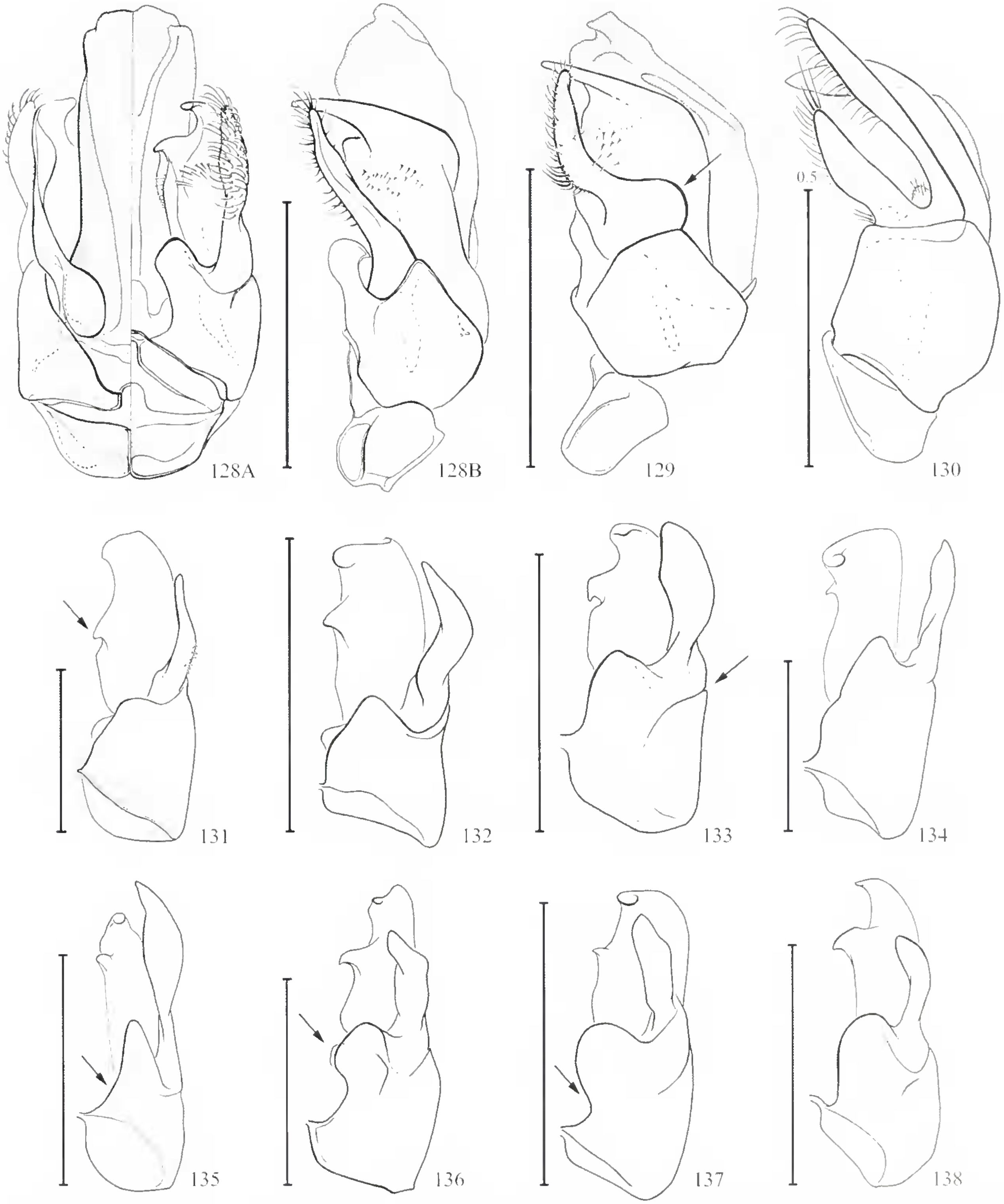
126 *Triepeolus nobilis*



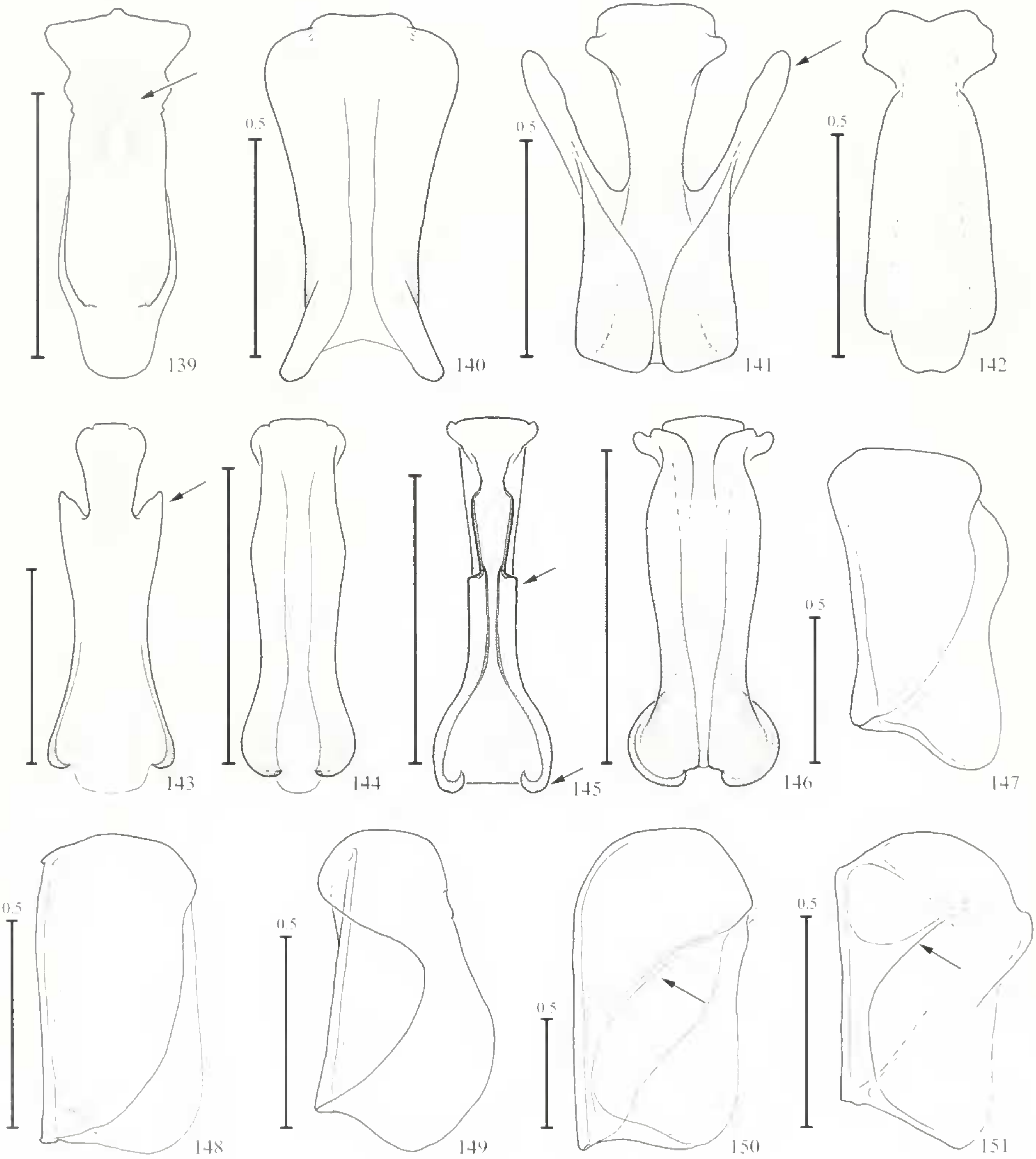
127 *Triepeolus vicinus*

1 mm

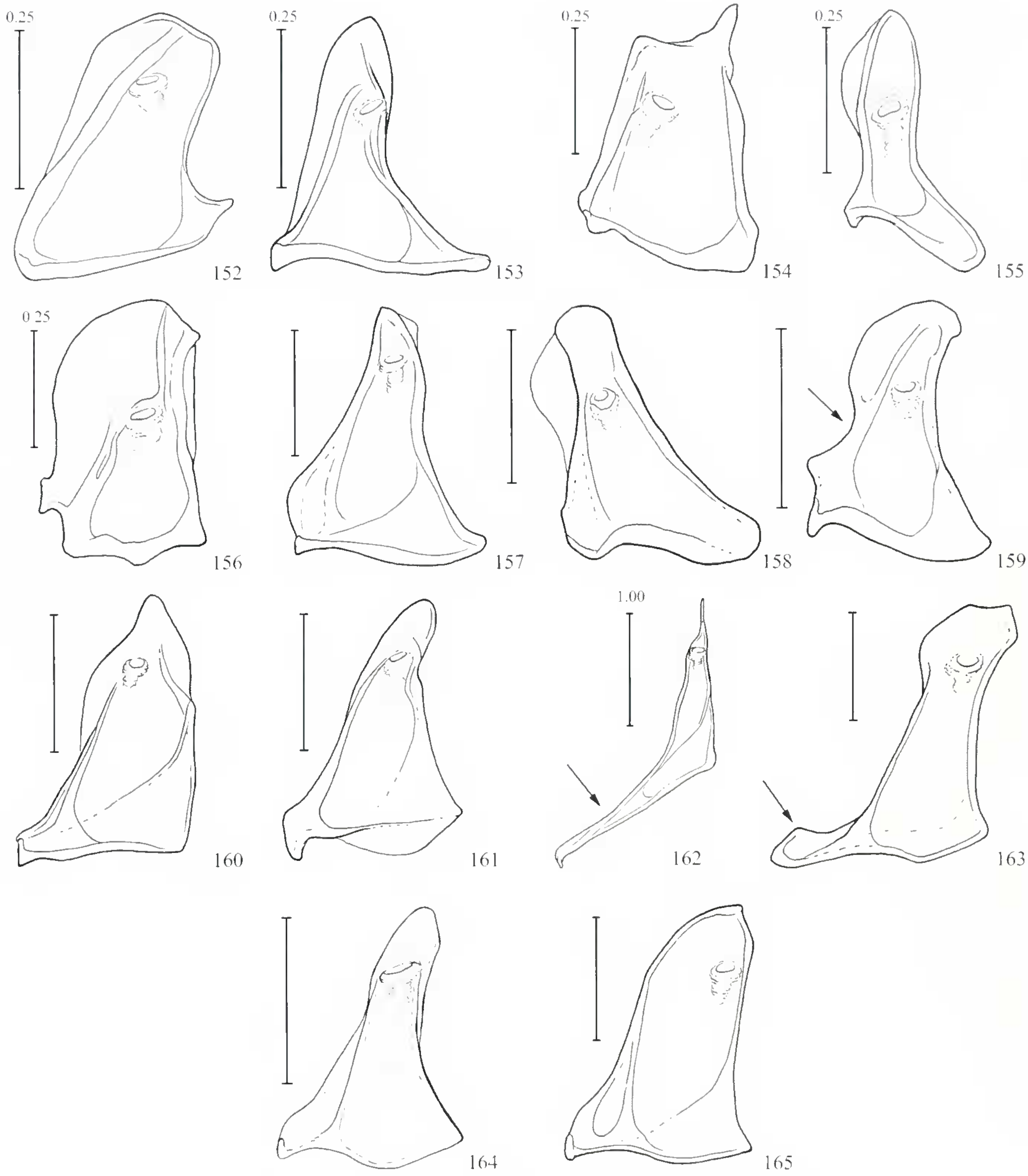
Figs. 119–127. Ventral view of male eighth sterna.



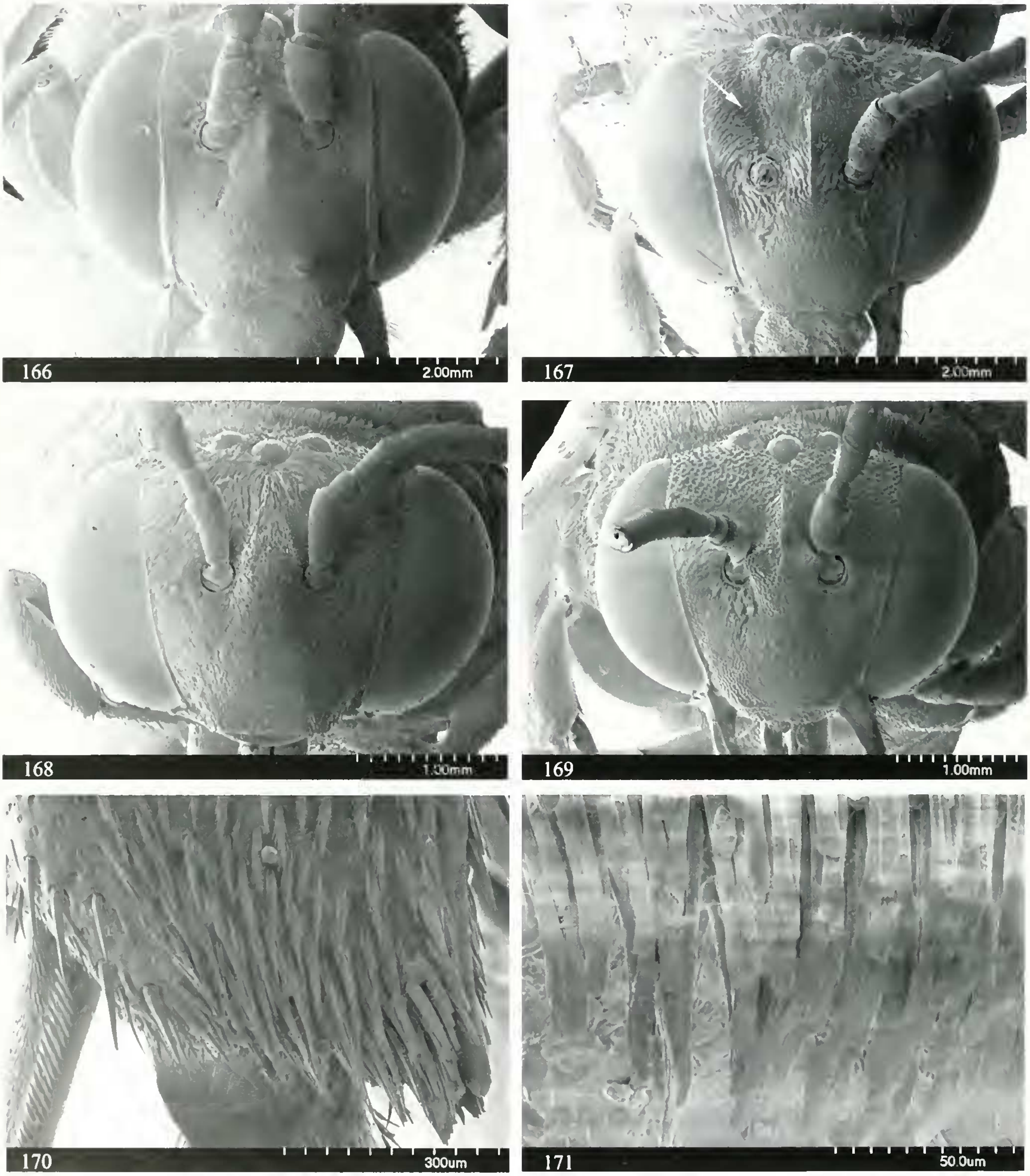
Figs. 128–138. Scale bars = 1 mm, unless otherwise indicated. Fig. 128. *Triepeolus epeolurus*, male genital capsule. A. Left, dorsal view; right, ventral view. B. Lateral view. Figs. 129 and 130. Lateral view of male genital capsules. 129. *Epeolus natalensis*, arrow pointing to basal lobe of gonostylus. 130. *Brachynomada scotti*, redrawn from Rozen (1997). Figs. 131–138. Right sides of male gonocoxites, right gonostyli, and right penis valves, ventral view (setae omitted except for stout setae on gonostylus of *Odyneropsis armata*). 131. *Odyneropsis armata*, arrow pointing to inner, medial projection of penis valve. 132. *Rhogepeolus bigibbosus*. 133. *Epeolus natalensis*, arrow pointing to lateral sulcus of the gonocoxite. 134 *Thalestria spinosa*. 135. *Rhinepeolus rufiventris*, arrow pointing to ventral margin of gonocoxite. 136. *Doeringiella crassicornis*, arrow pointing to lobe on inner surface of the gonocoxite. 137. *Pseudepeolus fasciatus*, arrow pointing to emarginate ventral margin of gonocoxite. 138. *Triepeolus tristis*.



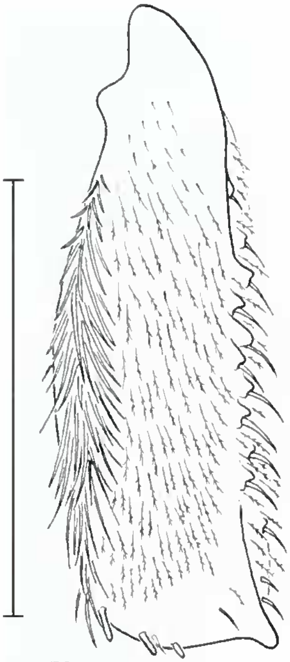
Figs. 139–146. Dorsal view of penes. Stippling indicates sclerotization. Scale bars = 1 mm, unless otherwise indicated. 139. *Odyneropsis batesi*, arrow pointing to median sclerotized plates. 140. *Rhogepeolus biggibosus*. 141. *Epeolus mesillae*, arrow pointing to lobe on lateral margin of penis. 142. *Epeolus bifasciatus*. 143. *Thalestria spinosa*, arrow pointing to subapical lamellate projection. 144. *Rhinepeolus rufiventris*. 145. *Doeringiella crinita*, arrows pointing to medial lamellate projection and highly recurved basal part of penis valve. 146. *Triepeolus ancoratus*. Figs. 147–151. Female eighth terga, lateral view. 147. *Odyneropsis batesi*. 148. *Rhogepeolus bigibbosus*. 149. *Epeolus cruciger*. Figs. 150 and 151. Arrows pointing to sclerotized cross bar extending from anterior ridge. 150. *Thalestria spinosa*. 151. *Triepeolus epeolurus*.



Figs. 152–165. Female seventh terga, lateral view (lateral processes oriented toward the right). Scale bars = 0.5 mm, unless otherwise indicated. 152. *Biastes brevicornis*. 153. *Brachynomada scotti*. 154. *Hexepeolus rhodogyne*. 155. *Holcopasites calliopsidis*. 156. *Nomada pampicola*. 157. *Odyneropsis armata*. 158. *Rhogepeolus bigibbosus*. 159. *Epeolus cruciger*, arrow pointing to emarginate lateral margin. 160. *Rhinepeolus rufiventris*. 161. *Pseudepeolus fasciatus*. 162. *Thalestria spinosa*, arrow pointing to extremely elongate lateral process. 163. *Doeringiella bizonata*, arrow pointing to elongate lateral process. 164. *Triepeolus epeolurus*. 165. *Triepeolus tristis*.



Figs. 166–169. Faces of Epeolini. 166. *Odyneropsis armata*. 167. *Doeringiella crassicornis*, arrow pointing to depression on frons. 168, *Rhinepeolus rufiventris*. 169. *Epeolus tarsalis rozenburgensis*. Figs. 170 and 171. Setae of outer posterolateral corners of mesotibiae. 170. *Triepeolus quadrifasciatus*. 171. *Epeolus schummeli*.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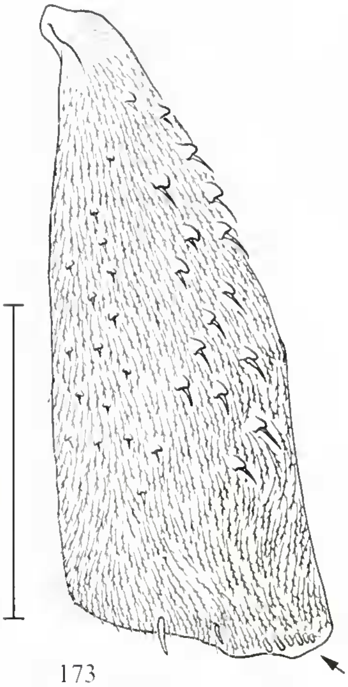
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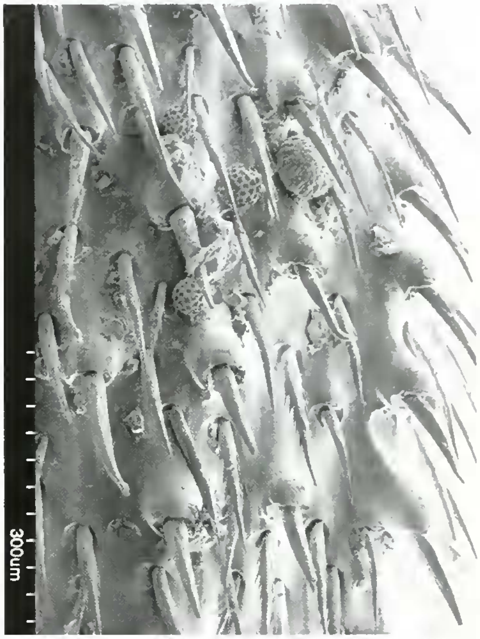

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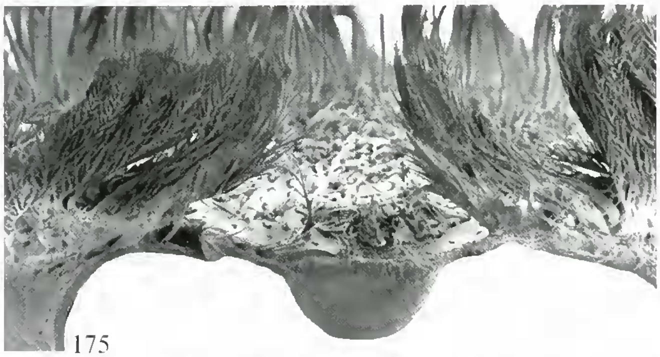
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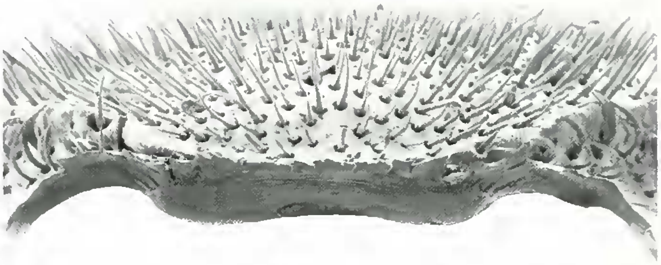
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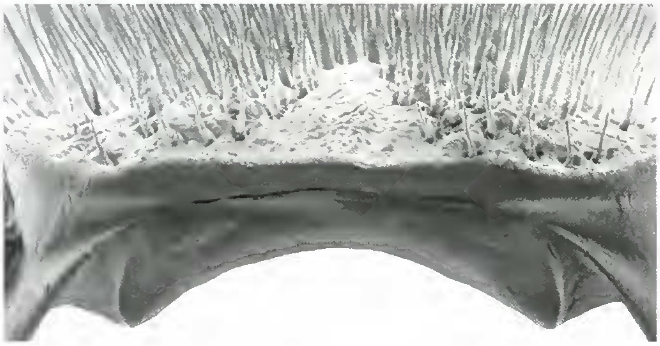
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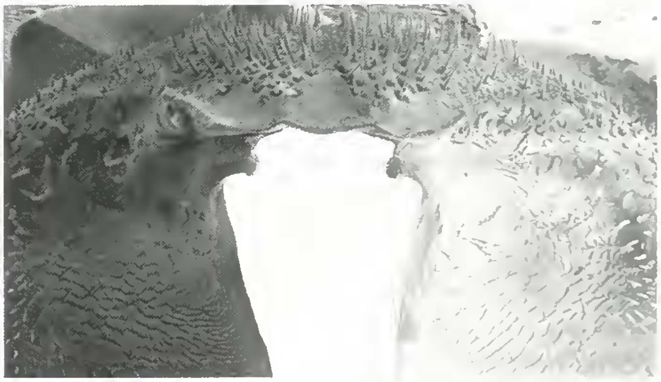
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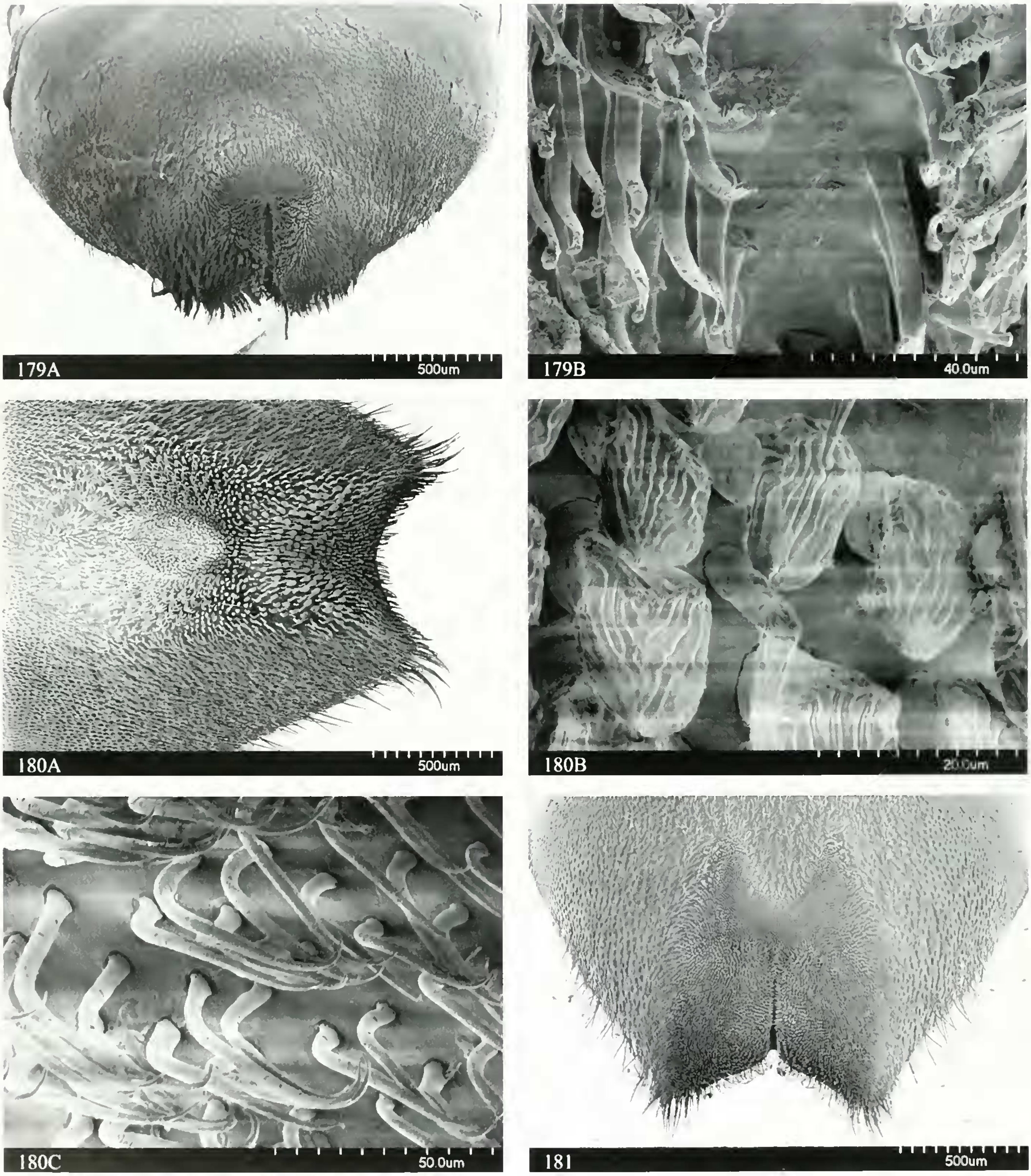
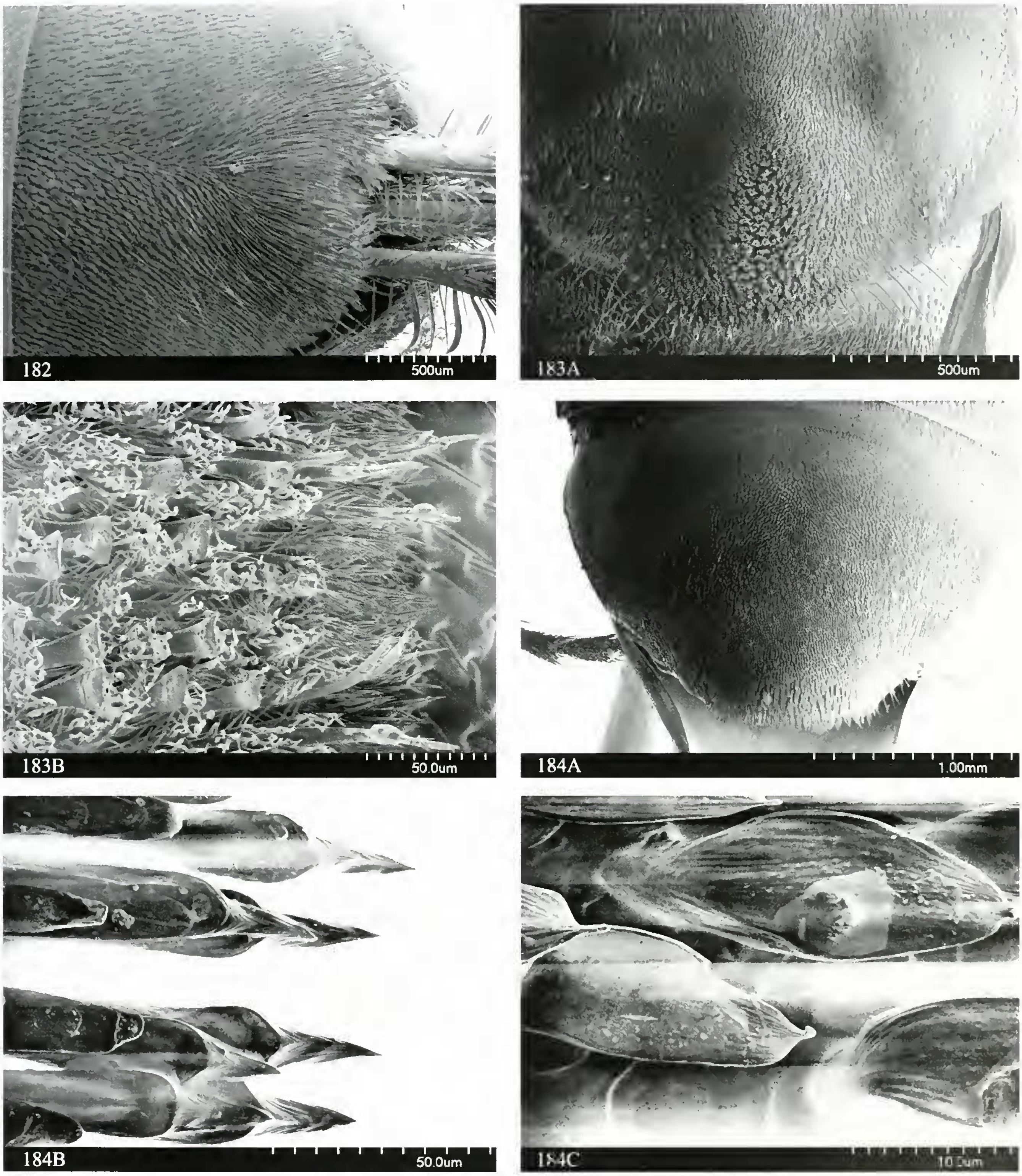
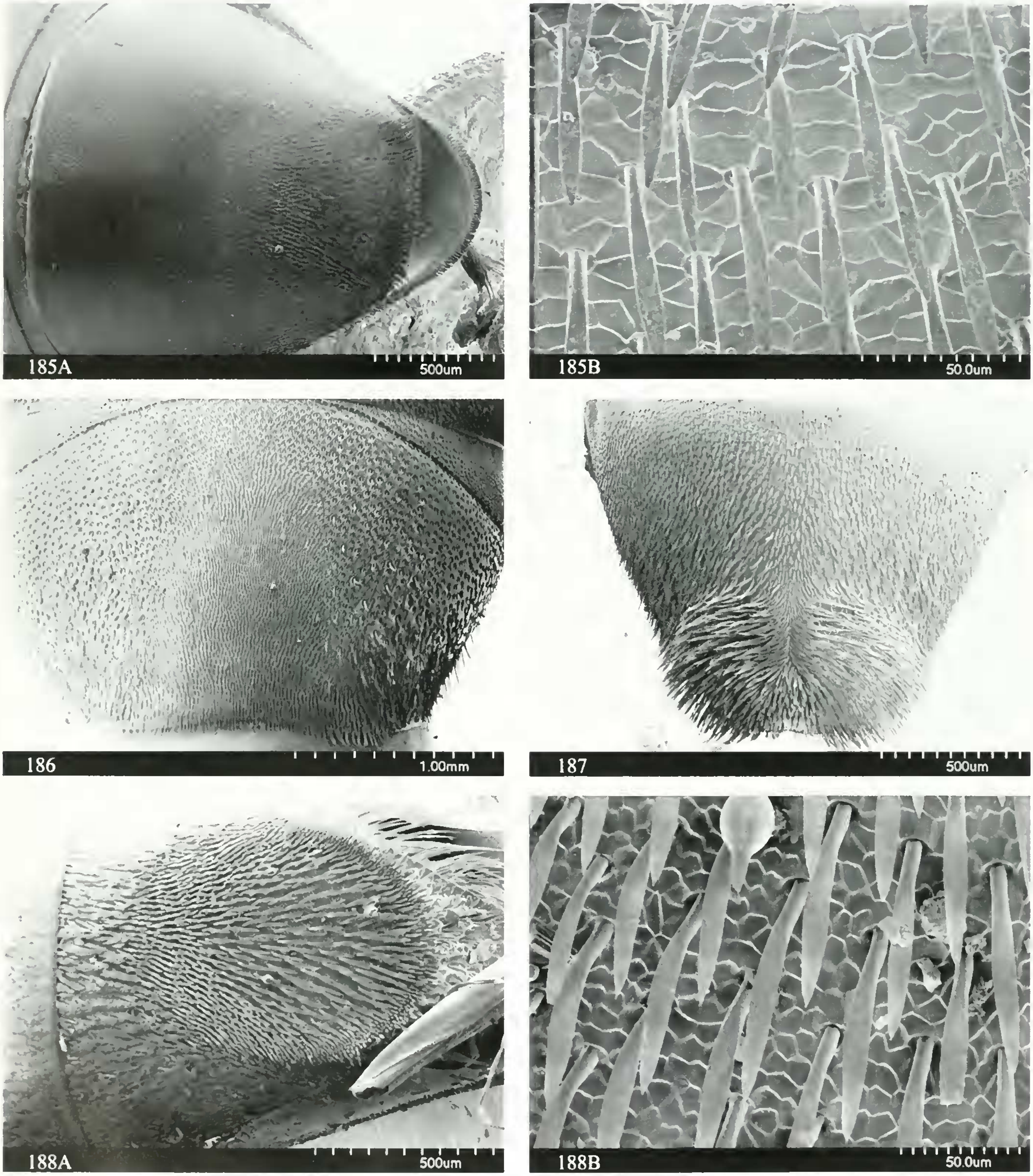
Figs. 172 and 173. *Rhogepeolus emarginatus*. 172. Mesotibia. 173. Metatibia, arrow pointing to stout setae. Fig. 174. *Triepeolus quadrifasciatus* metatibia, detail of spine-like setae. Figs. 175–178. Posterior view of apical margins of female sixth sterna, including pygidial plates. 175. *Thalestria spinosa*. 176. *Epeolus compactus*. 177. *Rhogepeolus bigibbosus*. 178. *Doeringiella crinita*.



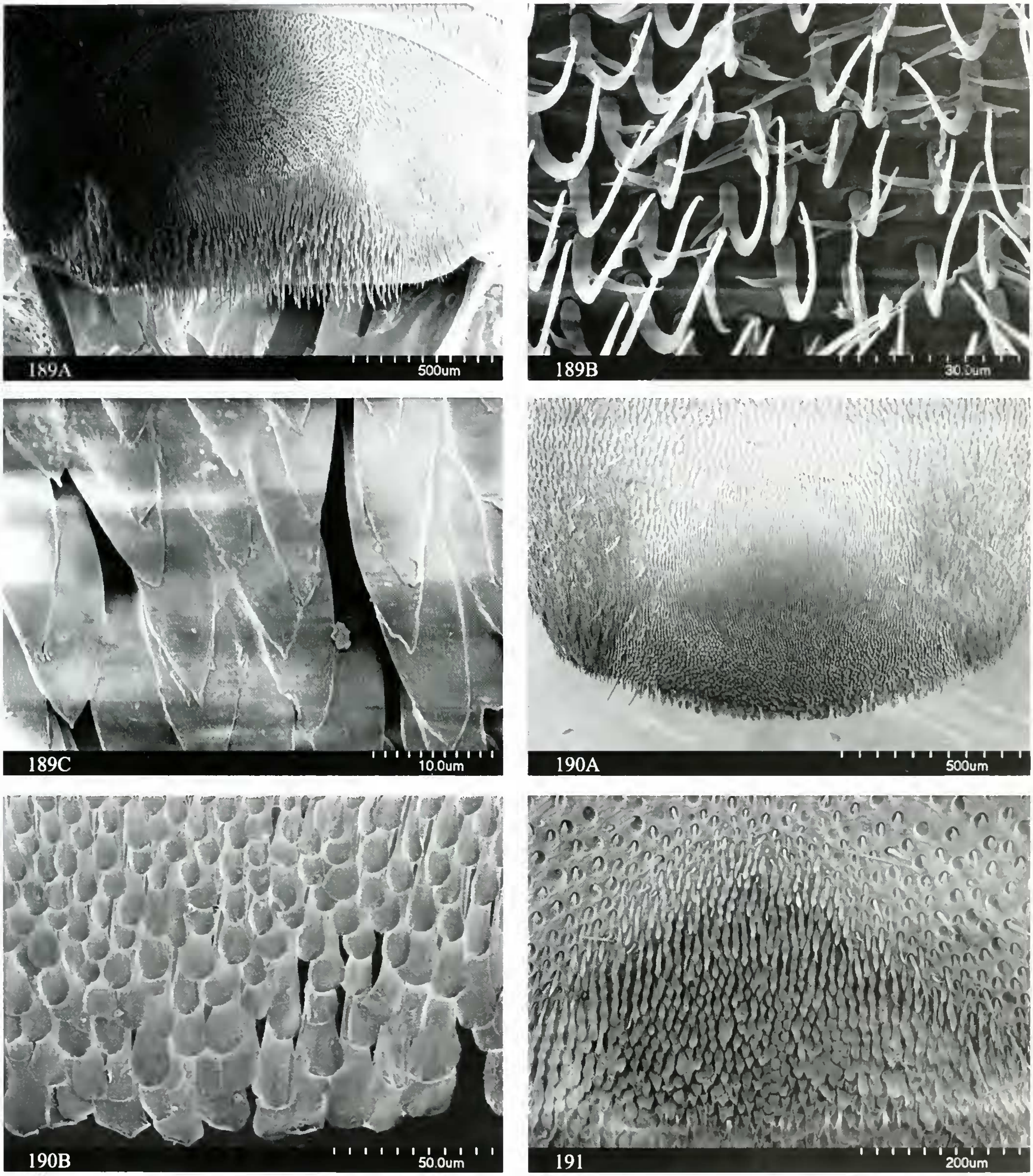
Figs. 179–181. Female pseudopygidial areas. 179. *Rhogepeolus biggibosus*. A. Dorsal view of T5. B. Detail of setae bordering longitudinal apical slit. 180. *Odyneropsis armata*. A. Dorsal-posterior view of T5 (posterior directed right). B. Detail of setae creating "carina" of circular depression. C. Detail of setae lateral to circular depression. 181. *Odyneropsis batesi*, dorsal-posterior view of T5.



Figs. 182–184 Female pseudopygidial areas. 182. *Thalestria spinosa*, dorsal-posterior view of T5 with S6, gonoplacs, and sting partially visible (posterior directed right). 183. *Rhinepeolus rufiventris*. A. Dorsal-posterior view of T5. B. Detail of apical longitudinal region of stout setae (posterior directed right). 184. *Pseudepeolus fasciatus*. A. Dorsal-posterior view of T5. B. Detail of medioapical setae (posterior directed right). C. Detail of setae basal on pseudopygidial area (posterior directed right).



Figs. 185–188. Female pseudopygidial areas. 185. *Doeringiella crinita*. A. Dorsal view of T5 (posterior directed right). B. Detail of setae medially on pseudopygidial area. 186. *Triepeolus distinctus*, dorsal view of T5. 187. *Triepeolus heterurus*; dorsal view of T5. 188. *Triepeolus ancoratus*. A. Dorsal view of T5 (posterior directed right). B. Detail of setae medially on pseudopygidial area.



Figs. 189–191. Female pseudopygidial areas. 189. *Triepeolus epeolurus*. A. Dorsal view of T5. B. Detail of setae basal on pseudopygidial area, adjacent to median region of flattened setae. C. Detail of flattened setae forming transverse region medially on pseudopygidial area. 190. *Epeolus lectoides*. A. Dorsal view of T5. B. Detail of flattened setae on apical margin of pseudopygidial area. 191. *Epeolus bifasciatus*, dorsal view of pseudopygidial area.